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Author: Jan Plue, Sara A. O. Cousins, Karen De Pauw, Martin Diekmann, Jenny Hagenblad, Kenny Helsen, Anna Orczewska i in.

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Biological Flora of the British Isles: *Poa nemoralis*

Jan Plue¹ | Sara A. O. Cousins¹ | Karen De Pauw² | Martin Diekmann³ |
 Jenny Hagenblad⁴ | Kenny Helsen⁵ | Martin Hermy⁶ | Jaan Liira⁷ | Anna Orczewska⁸ |
 Thomas Vanneste² | Monika Wulf⁹ | Pieter De Frenne²

¹Biogeography and Geomatics, Department of Physical Geography, Stockholm University, Stockholm, Sweden; ²Forest & Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Melle-Gontrode, Belgium; ³Vegetation Ecology and Conservation Biology, Institute of Ecology, University of Bremen, Bremen, Germany; ⁴Department of Physics, Chemistry and Biology, Linköping University, Linköping, Sweden; ⁵Plant Conservation and Population Biology, Biology Department, University of Leuven, Heverlee, Belgium; ⁶Division of Forest, Nature & Landscape Research, University of Leuven, Heverlee, Belgium; ⁷Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia; ⁸Faculty of Natural Sciences, Institute of Biology, Biotechnology and Environmental Protection, University of Silesia, Katowice, Poland and ⁹Centre for Agricultural Landscape Research (ZALF), Müncheberg, Germany

Correspondence

Jan Plue

Email: jan.plue@natgeo.su.se

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Abstract

1. This account presents information on all aspects of the biology of *Poa nemoralis* L. (Wood Meadow-grass) that are relevant to understanding its ecological characteristics and behaviour. The main topics are presented within the standard framework of the *Biological Flora of the British Isles*: distribution, habitat, communities, responses to biotic factors, responses to environment, structure and physiology, phenology, floral and seed characters, herbivores and disease, history, and conservation.
2. The grass *Poa nemoralis* is widespread and frequent to locally common across the British Isles, except for western and central Ireland, and northern Scotland. In both its native Eurasian range and introduced ranges in, for example, the Americas, its main habitat comprises temperate (mixed) deciduous woodland. The species finds important secondary habitats in hedgerows, as well as in non-woodland vegetation such as on cliffs, screes and walls or sporadically in grassland and heathland. Although not always taxonomically or morphologically distinct units, the species is suspected to comprise many cytological races and hybrid polyploid populations with variable morphology. Morphological variation among *P. nemoralis* populations may also be a sign of local environmental adaptation or a result of introgressive hybridization with other, morphologically variable members of *Poa* section *Stenopoa* such as *P. glauca*, *P. compressa* or *P. pratensis*.
3. *Poa nemoralis* is a small-statured, loosely caespitose grass, with populations ranging from a few individual tufts to those visually defining the aspect of the herbaceous understorey. The species tolerates moderate to deep shade on the forest

*Nomenclature of vascular plants follows Stace (2019) and, for non-British species, *Flora Europaea*.

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floor, yet it tends to forage for available light, occurring more and growing taller in canopy gaps, forest edges and hedgerows. The amount of light is central to its survival and reproductive ecology, being important for flower induction, seed production and seed germination. The species produces large quantities of small, light seeds which facilitate spatial and temporal dispersal.

4. The species occupies a wide range of soil pH (3–7) and nutrient conditions (C/N ratio ranges between 10 and 25), though it clearly prefers moderately acid and somewhat drier soils with limited litter thickness, avoiding soils with mor humus types. *Poa nemoralis* displays distinct small-scale acidifuge responses, being absent in areas of low soil pH (<3).
5. *Poa nemoralis* is a moderately strong indicator of ancient woodland: it can quickly colonize recently established wooded areas adjacent to ancient woodland when it is not hindered by dispersal limitation and elevated nutrient levels. Nonetheless, dispersal limitation impedes rapid colonization of isolated, recently established woodlands, in spite of ample records of zoochorous seed dispersal. While currently frequent to locally common, the species is at risk if ancient woodlands continue to decline in its native Eurasian range. Across N.W. Europe, it is already in moderate decline in temperate deciduous ancient woodlands because of acidification, eutrophication and darkening of the forest understorey. In its introduced ranges, it is considered invasive.

KEYWORDS

climatic limitation, communities, ecophysiology, geographical and altitudinal distribution, germination, herbivory, mycorrhiza, reproductive biology

Wood Meadow-Grass. Poaceae. *Poa*, section *Stenopoa* Dumort. *Poa nemoralis* is a loosely caespitose, perennial grass with epigeogeneous rhizomes. Branching of vegetative shoots basal, all or mostly extravaginal. Culms to (15)30–80(90) cm, mostly erect, sometimes geniculate, slender, smooth below the panicles, 3–5 noded; nodes slightly compressed, turning from green to light brown at maturity, the top node positioned at c. 1/2–3/4 of the culm length. Culms terminating in a slender to moderately stout panicle, with 2–6 ascending to widely spreading branches. Sheaths terete, closed for the lower 10%–20%; bases of basal sheaths glabrous. Ligule (0.1)0.2–0.5(1) mm long, sparsely to densely scabrous, apices truncate, minutely ciliate. Ligules comprising three cell types: elongated long cells, shorter long cells near edges and unicellular prickly hairs. Leaf blades 1–3 mm wide, lanceolate, mostly flat, 5–12 cm long, smooth or weakly rough, more or less abruptly ascending to spreading, straight or ultimately somewhat lax; apex abruptly acute or acute. Panicles (3)7–20 cm, usually erect, lax in shade forms, narrowly lanceoloid to ovoid, slightly to moderately congested; lowest nodes with 2–6 branches. Spikelets solitary, 2.6–4.0(8.0) mm, narrowly lanceolate to lanceolate, laterally compressed, usually not glaucous. Fertile spikelets pedicelled. Pedicels 0.5–6 mm long. Florets (1)2–5 per spikelet. Glumes persistent and slightly unequal, shorter than spikelet, lanceolate,

distinctly keeled, keels smooth or sparsely scabrous, apices sharply acute to acuminate. Lemmas 2.4–4.0 mm; proximal lemma narrowly lanceolate to lanceolate, distinctly keeled. Palea about as long as lemma, keels scabrous. Callus bearing distinctive webbed hairs. Anthers 3, 1–2 mm long. Caryopsis with adherent pericarp, enclosed in the hardened lemma and palea. The information in this section is mostly derived from Chaffey (1984), Hubbard (1984), Clayton, Vorontsova, Harman, and Williamson (2006), Barkworth, Capels, Long, Anderton, and Piep (2007), Cope and Gray (2009), Klimešová, Danihelka, Chrtěk, Bello, and Herben (2017), Mossberg and Stenberg (2018) and Stace (2019).

Wood Meadow-grass is a highly variable species that is widespread in temperate to subarctic parts of the northern hemisphere and a large number of subspecies and varieties have been recognized. Some variation is phenotypic, due to environmental variation in shade and moisture. Plants from deep shade are often weakly developed with 1- to 2-flowered spikelets, while more robust plants with 3- to 5-flowered spikelets grow in moister, lighter places. Mountain populations usually have loose panicles, with fewer and larger spikelets, and longer glumes and lemmas (Hubbard, 1984). The species comprises various cytotypes across its range (mostly diploid, tetraploid and hexaploid), which may form hybrid polyploid populations. The

Plant List (2019) reports no less than 104 named subspecies of *P. nemoralis* within and outside of its native Eurasian range. Most of these subspecies are not broadly accepted, except for the following four, according to the Euro + Med Plantbase (2006), which covers the Euro-Mediterranean region: subsp. *alexeeenkoi* Tzvelev, subsp. *carpatica* V. Jirásek, subsp. *hypanica* (Prokudin) Tzvelev and subsp. *lapponica* (Prokudin) Tzvelev. Subspecies may therefore mostly be indicative of local environmental adaptation in morphology resulting from phenotypic plasticity, rather than being genetically distinct. Examples of subspecies accepted within Switzerland and their associated morphological variation include subsp. *vulgaris* (small spikelets, 3–4 mm long, with 1–3 flowers), subsp. *montana* (large spikelets, 5–6 mm long, with 3–5 flowers; usually <10 spikelets per inflorescence) and subsp. *glauca* (large, obtuse, glaucous spikelets with 5–6 flowers; Duckert-Henriod & Favarger, 1987). In the British Isles, no subspecies are currently recognized but difficulties are encountered in montane habitats where it is often difficult to differentiate between *P. nemoralis* and shade forms of *P. glauca* (*P. balfouri*; Cope & Gray, 2009; Trist, 1986). In North America, two subspecies are documented: *P. nemoralis* subsp. *interior* (Rydb.) W.A. Weber, which is considered native (and potentially a species in its own right; Rydberg, 1905) and *P. nemoralis* subsp. *nemoralis*, which is allegedly introduced (CABI, 2020).

Poa nemoralis is a graceful native grass, widespread and locally abundant throughout much of the British Isles, in woodlands, hedgerows and other shady habitats, such as banks and glades on different soil types. A form also occurs in drier places such as on walls and rock ledges in mountains. It is probably introduced to parts of north-west Britain, the Isle of Man and Ireland.

1 | GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

Poa nemoralis is locally abundant throughout most of southern Britain in woodlands and hedgerows becoming much rarer in northern Britain and Scotland and in lowland areas where wooded habitats are scarce such as in the Fenlands (i.e. the southern parts of Lincolnshire and in the northern parts of Cambridgeshire). In Britain, the species occurs in 1960 of the 2,805 10 km × 10 km grid squares (hectads), and in five of the 14 UTM grid squares (hectads) covering the Channel Islands (Figure 1; Hill, Preston, & Roy, 2004). In Ireland, it occurs locally, mainly in the east. *Poa nemoralis* is probably introduced in Ireland, the Isle of Man and north-west Britain, via grassland mixtures intended for sowing in shady places (Allen, 1964; Clapham, Tutin, & Warburg, 1989; Cope & Gray, 2009; Hubbard, 1984; Stace, 2019).

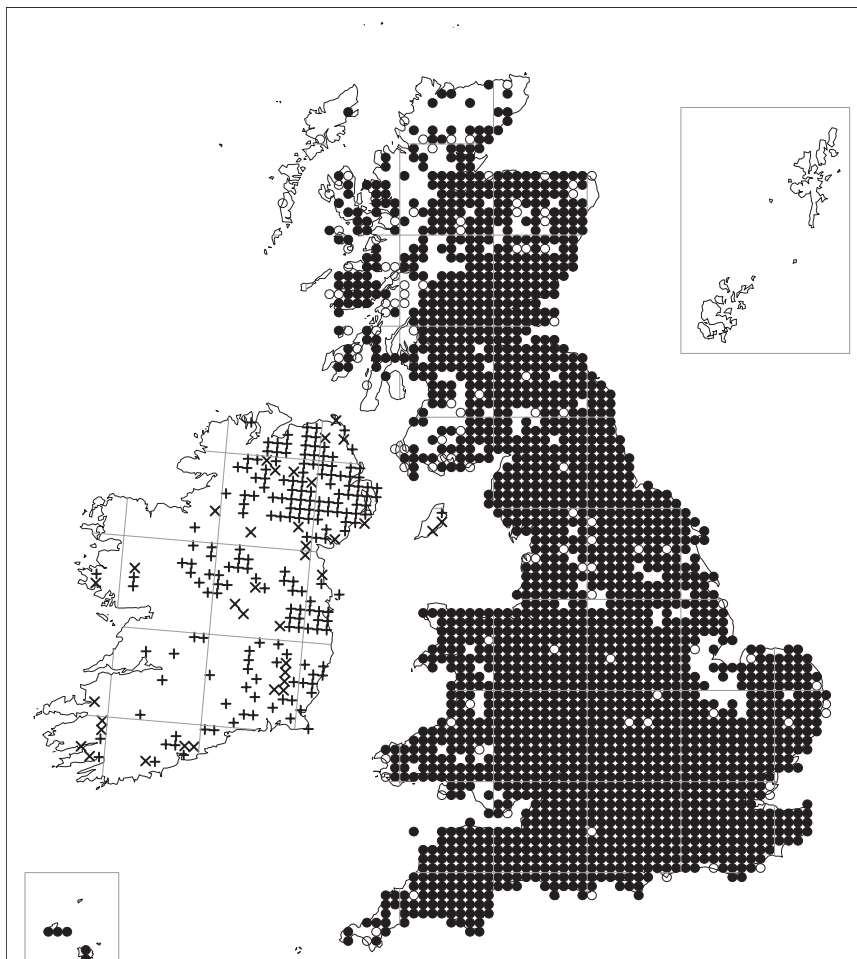


FIGURE 1 The distribution of *Poa nemoralis* L. in the British Isles. Each dot represents at least one record in a 10-km square of the National Grid. (●) Native 1970 onwards; (○) native pre-1970; (+) non-native 1970 onwards; (x) non-native pre-1970. Mapped by Dr Kevin Walker, of the Botanical Society of Britain and Ireland, mainly from records collected by its members, using Dr A. Morton's DMAP software

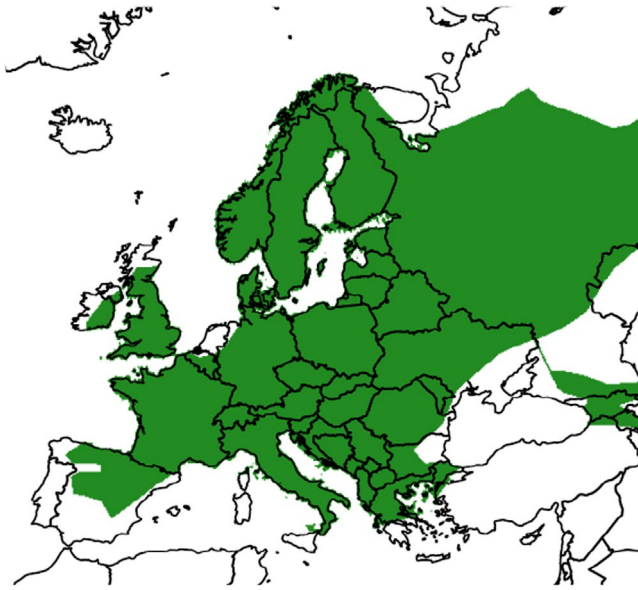


FIGURE 2 The distribution of *Poa nemoralis* L. in Europe and neighbouring areas using a Lambert Azimuthal Equal Area projection and resolution of 10 km × 10 km (redrawn after Hultén & Fries, 1986). While the distribution in Ireland was mapped as native in Hultén and Fries (1986), this is inconsistent with other sources suggesting that the Irish records are non-native. See Figure 1 for the distribution of *Poa nemoralis* in the British Isles [Colour figure can be viewed at wileyonlinelibrary.com]

Poa nemoralis is classified as a member of the Circumpolar Boreo-temperate floristic element by Preston and Hill (1997) and is found over much of the European continent, from Iceland and the North Cape in northernmost Scandinavia, eastward to the Ural Mountains, and south to the Mediterranean and the Black Sea (Figure 2). In northern Europe, it occurs on the Faroe Islands and Greenland (Daniëls, 1982; Kartesz, 2015; Mossberg & Stenberg, 2018), but not on Svalbard (Mossberg & Stenberg, 2018). In Scandinavia, *P. nemoralis* is common up to latitudes of 70°N (Hultén & Fries, 1986). Towards southern Europe, *P. nemoralis* is more sparsely distributed and it is absent from most of the Mediterranean region, except in uplands and mountains (e.g. the Pyrenees, Alps, Apennines and on Corsica and Sardinia). The southern range limits in Europe are around 38°N in Spain and Italy. Outside Europe, the species extends south into the mountains of north Africa and east across Turkey and the Caucasus through to parts of Siberia and the mountains of central Asia to Kamchatka, China and Northern Japan.

Poa nemoralis subsp. *nemoralis* has been introduced to North America from northern Eurasia (Barkworth et al., 2007). *Poa nemoralis* subsp. *interior* is considered native but might better be accepted as a separate species, *P. interior*, given its morphological distinctiveness (Rydberg, 1905). The North American *P. nemoralis* subsp. *nemoralis* is established primarily at low elevations in deciduous and mixed conifer/deciduous forests and has a wide range from Washington, British Columbia and Alaska in the west, across Alberta, Manitoba, Ontario, Québec and Wisconsin, Michigan and New York to the whole east coast from Newfoundland, Nova Scotia, New Brunswick

and Maine down to Virginia and North Carolina (Barkworth et al., 2007). According to Kartesz (2015), the species also occurs in California, Oregon, Saskatchewan, Idaho, North Dakota, Minnesota, Iowa and Missouri. In Wisconsin, the species increased in local abundance between 1950 and 2000 from being entirely absent to occupying 10% of 7,440 1-m² quadrats in forest stands where the species was recorded, representing a regional change from 0% to 8% of the 62 resampled forest stands being occupied (Wiegmann & Waller, 2006). It has also been reported in Australia and New Zealand (USDA-ARS, 2019), Argentinean Patagonia (Rua, 1996), Guatemala (Ortega-Olivencia & Devesa, 2018) and South Africa (Van Landuyt et al., 2006).

In the British Isles, *Poa nemoralis* occurs from near to sea level up to 915 m above sea level (a.s.l.) in Sgurr na Lappaich, Glen Farrar, Easternness, Scotland (Hill et al., 2004; Streeter, Hart-Davies, Hardcastle, Cole, & Harper, 2016). In Europe, the species is similarly found from around sea level in Belgium (Van Landuyt et al., 2006), France, the Netherlands and Sweden, up to 1,800 m a.s.l. in Italy (Pignatti, 1982), 2,600 m in France (Tison & de Foucault, 2014) and 2,980 m on the Iberian Peninsula (Ortega-Olivencia & Devesa, 2018). In a large-scale floristic inventory of woodland plant communities across five mountain ranges in France (the western Alps, northern Pyrenees, Massif Central, western Jura and Vosges), the maximal elevation where *P. nemoralis* was recorded in these mountain plots was 1,190, 1,185, 1,510, 2,250 and 2,150 m a.s.l. in the Vosges, Jura, Massif Central, northern Pyrenees and western Alps, respectively (Lenoir, Gegout, Marquet, Ruffray, & Brisse, 2008). On Corsica, the maximum elevation recorded in that dataset was 1,560 m a.s.l. (J. Lenoir, pers. comm.). In Norway, the elevational limit is 1,300 m a.s.l. in the Hardangervidda National Park and 500 m a.s.l. in northern Norway (Hultén & Fries, 1986).

2 | HABITAT

2.1 | Climatic and topographical limitations

The hecads occupied by native populations of *P. nemoralis* in the British Isles (Figure 1) are characterized by a mean annual precipitation of 1,015 mm and mean January and July temperatures of 3.2°C and 14.8°C, respectively (Hill et al., 2004). The climatic amplitude of *P. nemoralis* throughout its vast Eurasian range (c. 9 million km²) is considerable with a mean annual temperature across its range of 6.3°C (ranging from 2.1°C to 10.4°C). The average total precipitation across its range is c. 694 mm/year. The mean annual temperature of the growing season across the range is 13.4°C ($SD \pm 3.0^\circ C$; range 9.2–17.3°C) with an average amount of 373 mm of rainfall during the growing season (De Frenne et al., 2013). This essentially implies that the species appears to avoid extremely cold arctic and alpine areas, as well as the driest parts of southern Europe. However, it can be locally rare, in spite of suitable climatic conditions, in lowland regions with low woodland cover, and it can be occasionally found in open upland areas.

2.2 | Substratum

In accordance with the broad range of environmental conditions and forest communities in which *P. nemoralis* occurs, the species is encountered on many different soil types. It is most often found on cambisols and luvisols, and somewhat less frequently on regosols and lithic or rendzic leptosols (for details of soil types, see the World reference base for soil resources; FAO, 1998). Occasionally, *P. nemoralis* can also be found on soils of more extreme edaphic conditions, such as pelosols, stagnic luvisols and podzols. Accordingly, the species prefers mull humus and to a minor extent moder, but tends to avoid mor humus types (Falkengren-Grerup, 1995a).

Poa nemoralis thus occurs on soils with a wide range of pH values (Figure 3a.). In an extensive study across all deciduous woodland communities in the Harz mountains in Germany (Pflume, 1999), topsoil pH varied between 3.5 and 7.1 for sites with *P. nemoralis* when measured in H₂O, and 2.9 and 6.9 in KCl. Similar ranges were obtained for measurements in the humus layer (3.5 and 7.3, pH-H₂O; 3.0 and 6.9, pH-KCl). Across the deciduous woodlands of Boreo-nemoral Scandinavia, sites with *P. nemoralis* also spanned 4 pH units (3.1–7.1 in pH-KCl; Diekmann, 1994). *Poa nemoralis* is common along most of the soil pH gradient, with the highest frequencies from 3 to 4.5 (top soil, pH-KCl) and from 4 to 5.5 (humus layer, pH-KCl) in Germany, and from 4 and 5 (top soil, pH-KCl) in Boreo-nemoral Scandinavia (Falkengren-Grerup, 1995a),

suggesting a preference for intermediate pH conditions. The species appears absent from soils more acidic than pH-KCl 3. In North German hedgerows ($n = 34$), the pH range of 3.4–7.0 is congruent with the spectrum observed in woodlands (Litzka & Diekmann, 2017). The avoidance of highly acidic and infertile sites likely has physiological reasons. At pH values below 3, the soil chemical environment, particularly elevated proton, aluminium and iron concentrations may prove toxic to *P. nemoralis* (cf. Wittig & Neite, 1986). The species has nonetheless been shown to be quite insensitive to 1–2 weeks of elevated H⁺ and Al³⁺ concentrations in the soil solution (Quist, 1995). *Poa nemoralis* can, to a certain extent, cope with increased acidification due to its phenotypic plasticity, although there is no evidence of any genetic adaptation to acidified soils (Göransson, Andersson, & Falkengren-Grerup, 2009). Among typical woodland species, *P. nemoralis* is one of the more acid-tolerant plants, although not as tolerant to low pH and nitrate supply as *Deschampsia flexuosa* (Falkengren-Grerup & Tyler, 1993; Wittig & Neite, 1986).

The mean Ellenberg nitrogen values (also a general indication of a preference for soil fertility) show a similar preference for intermediate sites: the species is infrequent at values >6.5, most likely because here *P. nemoralis* cannot compete with taller-growing herbs forming dense carpets, especially in the most eutrophic beech and elm-ash forests. At values <3.5, on the other hand, the species is rare because the least fertile sites are also the most acidic ones.

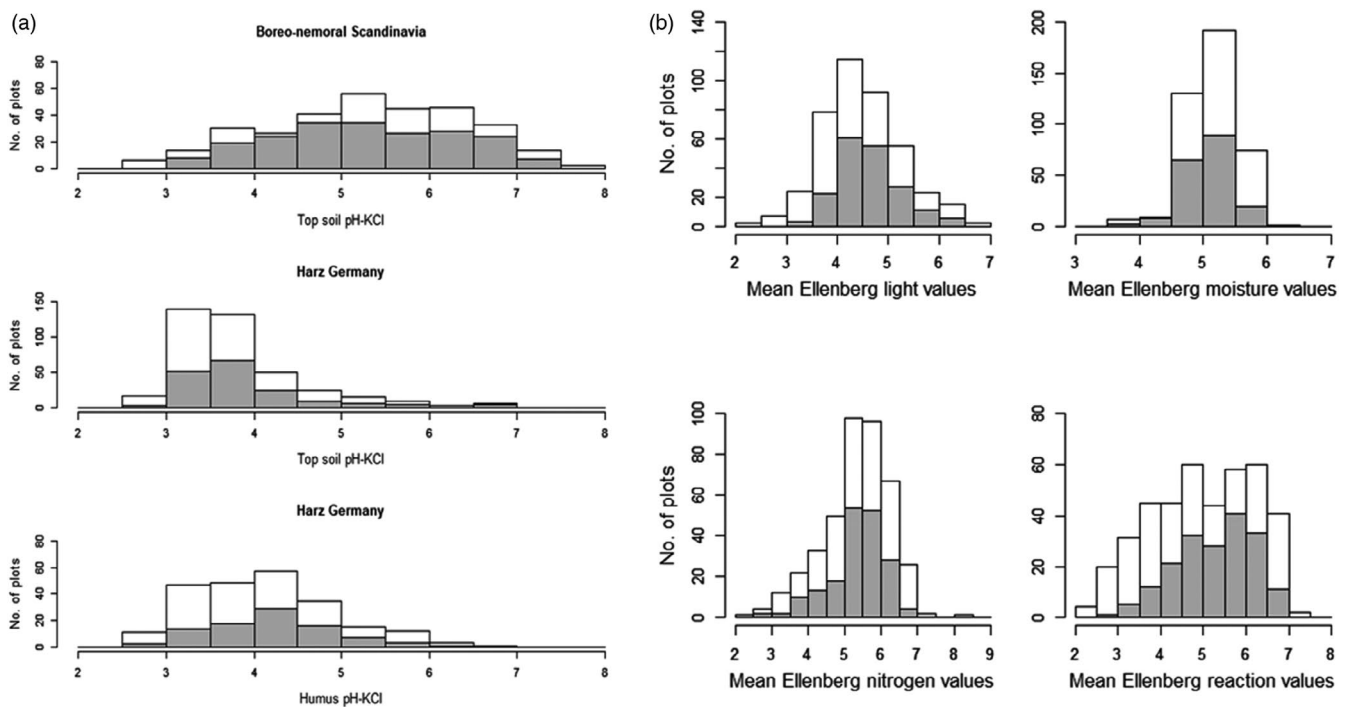


FIGURE 3 (a) The frequency distributions of soil pH-KCl values of all woodland sites (white bars) and woodland sites with the presence of *Poa nemoralis* (grey bars) across different woodland plant communities in Boreo-nemoral Scandinavia (top panel; topsoil pH, $n = 311$) and in the Harz mountains in Germany (middle panel, topsoil pH, $n = 401$; bottom panel, humus pH, $n = 229$). (b) Frequency distributions of the mean Ellenberg values for light (upper left panel), soil moisture (lower left panel), nitrogen (lower left panel) and soil acidity (lower right panel) of all woodland sites (white bars) and woodland sites with the presence of *Poa nemoralis* (grey bars) across different woodland plant communities in the Harz mountains in Germany. Data from Diekmann (1994) and Pflume (1999)

The mean Ellenberg moisture values show a slight preference of *P. nemoralis* for somewhat drier sites, in accordance with the literature (Diekmann, 1994; Mossberg & Stenberg, 2018). In summary, *P. nemoralis* prefers woodland sites with intermediate edaphic conditions, as expressed also in the Ellenberg scores for the British Isles ($F = 5$, $R = 6$ and $N = 5$; Hill et al., 2004) and similar scores for central Europe ($F = 5$, $R = 5$ and $N = 4$; Ellenberg & Leuschner, 2010).

The topsoil C/N ratio of woodland sites with *P. nemoralis* ranged between 10 and 25 with a mean of 18.6 in the Harz mountains (Pflume, 1999), aligning well with the species' preference for mull–moder humus types. Values below 10 (highly fertile sites) and above 30 (nutrient-poor environments) are almost absent. In highly fertile sites characterized by mull-humus types, significant interspecific competition likely limits the presence of *P. nemoralis* (Section 4). Alternatively, the lack of biotic perturbation, which gives rise to mor-humus types that it avoids, is due to highly acid, nutrient-poor conditions where the species encounters its physiological limitations. Soil organic matter content (loss on ignition, 650°C) across 264 deciduous woodland plots in southern Sweden occupied by the species averaged $14.0 \pm 7.4\%$, at a mean pH-KCl of 3.9 (Brunet, 1993).

3 | COMMUNITIES

In the British Isles, *Poa nemoralis* is found in dry woods, thickets, woodland rides and glades, hedgerows and other shady places, usually on well-drained soils and typically in the lowlands. It reaches its highest presence, and often the highest abundance, in *Fagus sylvatica*–*Mercurialis perennis* woodland (W12), especially in the *Sanicula europaea* subcommunity (Rodwell, 1991). However, its abundance in the *Fraxinus excelsior*–*Acer campestre*–*Mercurialis perennis* (W8) and in the *Quercus robur*–*Pteridium aquilinum*–*Rubus fruticosus* (W10) woodland types is also distinctive. Less commonly, it is a part of the *Fagus sylvatica*–*Rubus fruticosus* (W14), the *Fagus sylvatica*–*Deschampsia flexuosa* (W15) and the *Quercus petraea*–*Betula pubescens*–*Dicranum majus* (W17) woodland types (Rodwell, 1991). Although not explicitly mentioned, the species occurs in a broad range of other woodland communities and (remnant and/or linear) wooded habitats. *Poa nemoralis* is occasionally found on ungrazed ledges in the mountains where it grows with tall herbs such as *Alchemilla glabra*, *Angelica sylvestris* and *Geum rivale* in northern Britain (Pearman, Preston, Rothero, & Walker, 2008) or montane ledges co-occurring with herbs such as *Solidago virgaurea*, *Luzula sylvatica* and *Deschampsia cespitosa* in Scotland (Webster, Corner, Synnott, & Roger, 1970).

In Fennoscandia, *P. nemoralis* is common in shady deciduous and mixed woodlands, in groves, parks, but also in gorges and places adjacent to rock walls. In the European Habitat directive interpretation manual (EUR27, 2007), *Poa nemoralis* is indeed considered a typical species of Fennoscandian hemi-boreal, natural, old, broad-leaved deciduous woodlands (*Quercus*, *Tilia*, *Acer*, *Fraxinus* or *Ulmus* spp.), which are rich in epiphytes (9,020). Here it grows with species such as *Anemone nemorosa*, *Lathyrus vernus*, *Mercurialis perennis*, *Milium effusum* and *Polygonatum multiflorum*. Some of these woodlands were

formerly wooded meadows used for grazing or mowing that formed part of medieval infield systems (Depauw et al., 2019). Occasionally, *P. nemoralis* can occur in boreal herb-rich woodlands (groves), which are more open woodland types, partly due to former slash and burn cultivation (Hokkanen, 2003).

In Western Europe, *P. nemoralis* is rare in regions with very low woodland cover, such as the north of the Netherlands and the coastal areas of Belgium. It is linked to woodlands and particularly to forest edges, where it frequently occurs on the slopes of wooded banks, being considered a characteristic species of woodland edge communities (e.g. *Alliario-Chaerophylletum temuli*; Schaminée, Sykora, Smits, & Horsthuis, 2010). In Belgium, the Netherlands and northern France, it is associated with understorey communities in *Quercus robur* and *Q. petraea*–*Fagus* woodlands, as an important diagnostic species of *Querco-Fagetea* communities in general, and *Stellario-Carpinetum* communities in particular (Schaminée et al., 2010). *Poa nemoralis* is clearly less abundant towards the northwest and southwest of France (Julve, 2017), where it mostly occurs in the communities of both coniferous and deciduous forests.

In Central Europe, *P. nemoralis* occurs across a wide range of woodland communities on mesic soils, only avoiding woodlands on the driest and most nutrient-deficient sites (such as mixed thermophilic oak woodlands on steep calcareous slopes, or oak and beech woodlands on highly acidic soils) as well as alder *Alnus glutinosa* or birch *Betula pubescens* carr (Leuschner & Ellenberg, 2017). In most *Querco-Fagetea* communities, the species is relatively widespread and frequent, but it rarely attains dominance or cover values higher than 10%. *Poa nemoralis* is especially found in *Fagion* and *Carpinion* woodlands, and in woodlands rich in *Acer* spp., *Tilia* spp. and *Fraxinus excelsior* on highly fertile sites. It is, in contrast, less frequent in *Alno-Ulmion* woodlands (e.g. *Pruno-Fraxinetum* and *Carici remotae-Fraxinetum*) on moist soils (Döring-Mederake, 1991; Mast, 1999). *Poa nemoralis* often prefers sites below small openings in the canopy or the vicinity of lighter forest edges, while it is largely absent from the darkest places. It is absent from near-natural *Alnus glutinosa* swamp forests, except where the soil has been drained such as in the *Alnus glutinosa*–*Rubus idaeus* community (Mast, 1999).

In Eastern Europe, *P. nemoralis* is widely recorded both in open vegetation and in woodlands and thickets, particularly on more fertile, moist soils. It occurs in a wide range of woodland communities: alder woods (*Alnion glutinosae* with drier soil conditions later in the growing season, as opposed to permanently wet soils in Western Europe), different types of riverside communities (e.g. *Salicion albae*, *Alno-Padion*), oak–lime–hornbeam woodlands (*Carpinion betuli*), beech woodlands (*Fagion sylvaticae*), acidophilous and thermophilous oak woodlands (*Quercion robori-petraeae*), a Norway maple and large-leaved lime submountain community (*Aceri-Tilietum*), mountain sycamore (*Acerion pseudoplatani*) and beech–fir woodlands. *Poa nemoralis* is, however, rarely recorded in coniferous forests such as spruce, silver fir or pine forests (Chytrý & Rafajová, 2003; Kački & Śliwiński, 2012; Matuszkiewicz & Matuszkiewicz, 1996). *Poa nemoralis* is also mentioned in the European Habitat directive interpretation manual (EUR27, 2007) as a characteristic species of the Pannonian-Balkan

turkey oak–sessile oak woodland communities (91M0)—a subcontinental thermo-xerophile woodland type dominated by *Quercus cerris*, *Q. petraea* or *Q. frainetto*.

Poa nemoralis often attains high frequencies in hedgerow communities, for example in the British Isles (McCollin, Jackson, Bunce, Barr, & Stuart, 2000), the Netherlands (Stortelder, Schaminée, & Hommel, 1999) and Belgium (Deckers, Becker, Honnay, Hermy, & Muys, 2005; Vanneste et al., 2020). In Germany, it is one of the most common typical woodland species in hedgerows (Litzka & Diekmann, 2017; Wehling & Diekmann, 2010). In hedges in the northernmost part of the country in Schleswig-Holstein, the north-facing, more humid banks are characterized by the so-called *P. nemoralis* zone, shared with relatively light-demanding woodland plants such as *Stellaria holostea* and *S. nemorum* (Weber, 1967). Occurrences of the species in scrub and hedgerows have also been reported from the Mediterranean, for example in Italy (Pignatti, 1982). *Poa nemoralis* also occurs frequently in a range of non-woodland communities including vegetation on cliffs, screes and walls (calcareous and siliceous of either natural or anthropogenic origin), scrub and pioneer thickets of woodland clearings and thermophilous forest edge vegetation. Rare occurrences of *P. nemoralis* are also reported in a suite of grassland communities (dry, sandy, thermophilous, alpine and subalpine), around springs, in mires, heathlands and in nitrophilous ruderal vegetation (Chytrý & Rafajová, 2003; Kącki & Śliwiński, 2012).

4 | RESPONSE TO BIOTIC FACTORS

Poa nemoralis appears to have only limited capacity to withstand competition, as it tends to be excluded by above-ground interspecific competition (Conert et al., 1998; Hubbard, 1984). In two pot experiments using Russian knapweed (*Rhaponticum repens* (L.) Hidalgo) and a North-American congener (*P. secunda* J. Presl), *P. nemoralis* showed significant reduction in biomass when grown in competition with its *Poa* congener ($n = 10$; 40% reduction) and in competition with both its *Poa* congener and Russian knapweed ($n = 10$; >80%), compared to when grown alone (Ni, Schaffner, Peng, & Callaway, 2010). Furthermore, this biomass reduction was greater for *P. nemoralis* than for the eight other Eurasian forbs included in the experiment. This did not have an allelopathic cause, as root leachates from Russian knapweed induced the largest relative increase in *P. nemoralis* biomass ($n = 10$; 30% increase) compared to other Eurasian species (Ni et al., 2010). Nonetheless, in the herbaceous understorey of Hungarian woodland clearings, solitary individuals of *Achillea distans* and *Solidago virgaurea* significantly slowed the vegetative growth of the roots (>10 mm reduction within 10 days) and leaves (>4 mm reduction per 10 days) of *P. nemoralis*, through alleloinhibitory effects (Csontos, 1991). Additional evidence of competitive inferiority may be inferred from the observed expansion of its pH niche width towards northern latitudes. Reinecke et al. (2016) attribute this to the competitive release from neutrophilic species, which become less frequent.

Historically, *P. nemoralis* has been actively sown in woodlands as a means of providing extra fodder for grazing animals, and the species is known to be grazed and browsed by a suite of ungulates and small mammals (Hubbard, 1984; Section 9). Since the species can dominate the woodland understorey, it might be a reliable food source for these animals. However, the species seems unattractive as a food source, suggesting low palatability, given that the species is usually only consumed in small quantities (Section 9). Consequently, this would explain why occasional browsing is not really damaging (Klapp, 1983). However, frequent mowing (>1 cut per year; Klapp, 1983) or heavy grazing seems to affect *P. nemoralis* populations negatively. Relief from heavy grazing by fallow deer in the New Forest (Hampshire, UK) since 1961 led to recovery of *P. nemoralis* 22 years later, when it was exclusively present in enclosures for large grazing animals (Putman, Edwards, Mann, How, & Hill, 1989).

As a woodland understorey species, its light environment depends on the tree canopy. The mean Ellenberg light values indicate that *P. nemoralis* largely avoids darker woodlands or more shaded sites in woodlands with varying light fluxes at the forest floor (see also Diekmann, 1994; Tinya & Ódor, 2016). The species thus prefers intermediate levels of light (Ellenberg Indicator Value for $L = 4$ [British Isles; Hill et al., 2004] and 5 [Europe; Ellenberg, 1988]; Figure 3b). This is also reflected in its increased abundance at forest edges, in partly cleared woodlands and in hedgerows. Indeed, in an in situ mesocosm experiment in which the ambient light flux of $7.8 \mu\text{mol s}^{-1} \text{m}^{-2}$ was artificially enhanced to $31.8 \mu\text{mol s}^{-1} \text{m}^{-2}$ (equivalent to the creation of a small forest gap under closed forest canopy conditions; Rothstein & Zak, 2001), Blondeel et al. (2020) recorded a relative increase in the abundance of *Poa nemoralis* of 58% after 25 months. Mean plant height, however, remained unaffected: 22.3 ± 1.0 cm (SE; $n = 142$) versus 24.5 ± 1.4 cm (SE; $n = 159$).

Consequently, woodland management that opens up the overstorey canopy tends to yield positive effects on *P. nemoralis*. In a temperate deciduous forest in Hungary, with an overall mean cover of *P. nemoralis* of 2.34%, Tinya et al. (2019) compared the effects of a series of different canopy harvesting techniques. When a canopy gap was created by removing all trees in a circle 20 m in diameter, *P. nemoralis* cover increased from 2.34% to 10%. However, when 6–12 trees were retained in similar-sized 20 m-diameter canopy gaps, cover of *P. nemoralis* did not change. Cover of *P. nemoralis* did not change either in circular canopy gaps of 80 m in diameter in which all trees were clear-cut. However, in canopy gaps of 80 m in diameter in which only 30% of the basal tree area was removed, *P. nemoralis* cover did increase up to 30%. These positive responses could be related to increasing levels of both relative diffuse light availability (1.27% under closed canopy vs. 30.17% across treatments, relative to nearby open light conditions) and relative soil moisture content (−1.76% closed canopy vs. 2.41% across treatments, relative to nearby closed reference stands). Conversely, neither low nor high intensity coppicing in *Quercus robur*–*Q. petraea* forests in the Czech Republic seemed

to affect *P. nemoralis* cover, as it attained high cover even under closed oak canopies (Hédl, Šipoš, Chudomelová, & Utinek, 2017; see also Strubelt, Diekmann, Griesse, & Zacharias, 2019). Tree species identity did, however, affect *P. nemoralis* cover, as deeper shade in *Tilia cordata* coppices seemed to exclude *P. nemoralis* altogether (Hédl et al., 2017). In summary, it can be concluded that various biotic factors controlled by woodland management, such as the canopy density or dominant tree species, determine light conditions on the forest floor, directly or indirectly affecting the dynamics of *P. nemoralis* in the understorey.

5 | RESPONSE TO ENVIRONMENT

5.1 | Gregariousness

Poa nemoralis is a loosely tufted grass whose tussocks may be scattered in response to heterogeneous light availability (Tinya & Ódor, 2016), but it can also become so abundant that it defines the visual aspect of the woodland understorey (e.g. Hédl et al., 2017).



FIGURE 4 The growth form, adventitious root system (R) and the epigeogeneous rhizomes (rh) in *Poa nemoralis*. Scale bar represents 1 cm. Horizontal lines indicate the soil surface. Black tiller bases are dead plant material from preceding years. Reproduced with permission by Jitka Klimešová from Klimešová (2018)

Clonal growth in *P. nemoralis* is by means of epigeogeneous rhizomes: above-ground horizontal stems that can be pulled below-ground by adventitious root contraction (Figure 4; Klimešová et al., 2017). As a result, single tussocks usually consist of multiple structural individuals, that is, clonal tillers attached to one another (Wilhelm, 1995). Three small *P. nemoralis* tussocks consisted of an average of 7.6 clonal tillers, though there was large variation in the numbers of clonal tillers between tussocks (coefficient of variation of 108%; quantified using Italian plant material). Clonal propagation takes place when an individual tiller is severed by means of tussock fragmentation (Wilhelm, 1995). On average, the persistence of the physical connection by means of the epigeogeneous rhizomes is c. 3.5 years (Klimešová et al., 2017).

5.2 | Performance in various habitats

Poa nemoralis is traditionally considered an ancient woodland indicator in large parts of the British Isles and elsewhere in Europe (see Section 11). This implies that its reproductive and dispersal trait syndromes tend to confine its landscape-scale distribution to ancient woodlands, that is, woodlands with continuous forest cover: at least 150–200 years across large parts of Europe (De Frenne et al., 2013), although at least c. 400 years in the British Isles (Peterken & Game, 1984). A recent meta-analysis challenges this status, showing that the species' affinity to ancient woodland may only be moderate. The frequency of occurrence is only 1.65 times higher in ancient woodlands compared to recently established woodlands, making it a slightly faster than average colonizer of such recent woodlands (De Frenne et al., 2011). Studies in southern Sweden and Denmark confirm that the species can colonize recently established woodlands relatively quickly where they are adjacent to ancient woodland (Brunet, Frenne, Holmström, & Mayr, 2012; Graae, 2000), facilitated by its temporal and spatial dispersal capabilities (Section 8). However, in fragmented landscapes where recently established woodlands are isolated, Jacquemyn, Butaye, and Hermy (2001) confirmed that the distribution of *P. nemoralis* was significantly spatially clustered, presenting strong evidence for dispersal limitation. Furthermore, Kolk, Naaf, and Wulf (2017) established that *P. nemoralis* is significantly rarer in isolated, post-agricultural woodland fragments in the Prignitz region of north-eastern Germany. Peterken and Game (1984) equally convincingly established that *P. nemoralis* was primarily found in ancient woodlands (79% of the woodland localities), by inventorying isolated ancient and recent woodlands across Lincolnshire. Consequently, *P. nemoralis* may not suffer from recruitment limitation resulting from high nutrient status in post-agricultural woodland, as other ancient woodland indicators do (Baeten, Hermy, & Verheyen, 2009). However, dispersal limitation in fragmented woodland landscapes does seem to pose a significant problem for the species, including in the British Isles (Peterken & Game, 1984), justifying the general notion of the species as (moderately) indicative of ancient woodland. Older historical legacies within ancient woodlands may also

affect the distribution of *P. nemoralis*, as higher frequencies of *P. nemoralis* tie-in with the presence of ancient land uses, likely caused by higher nutrient status. Examples are seen in medieval in-field systems in southern Sweden (i.e. heavily manured lands used for crop production or managed as semi-open wooded meadows, Depauw et al., 2019) and in former Gallo-Roman settlements in northern France (i.e. islands made up of calcareous building materials embedded within an acid forest matrix, Plue et al., 2008).

Although *P. nemoralis* has shown a minor decline in ancient deciduous woodlands across its European range during recent decades (Section 11), acidification may cause more noted regional and local changes. In southern Sweden, continued acidification and loss of base cations in the woodland understorey over a 60-year period (−0.65 pH units between 1929 and 1988) appear to have driven a >50% increase in the frequency of *P. nemoralis* (227 occurrences across 526 deciduous woodland plots, 50 percentile of occurrences at pH-H₂O 4.1; Falkengren-Grerup, 1995a). Conversely, Naaf and Kolk (2016) found *P. nemoralis* to be a clear 'loser' species, having declined dramatically over a 50-year period (1960–2014), potentially due to acidification in all pH buffer ranges (Al-Fe buffer range, 14 occurrences in 1960 decreased to one occurrence in 2016; cation exchange buffer range, seven down to two occurrences; carbonate buffer range, two down to zero occurrences) based on re-surveys of 180 semi-permanent plots in deciduous woodlands in north-eastern Germany.

Even if root and shoot growth remain unaffected by short exposure to experimentally induced low soil pH (3.8) and high Al³⁺ concentrations (20 µM; Quist, 1995), small-scale soil heterogeneity in pH, with sustained low pH, can trigger acidifuge responses in the small-scale distribution of *P. nemoralis* on the forest floor. Wittig and Neite (1986) demonstrated how strong reductions in soil pH-H₂O (5.54 to 4.43) with parallel increases in Al³⁺ (mean of 4.17–25.77 mg/100 g dry soil) and Fe²⁺ ions (mean of 2.58–21.42 mg) significantly reduced the abundance of *P. nemoralis* (by 57%–75%) in response to stem flow from *Fagus sylvatica* tree trunks.

Other environmental changes in the woodland understorey may also be responsible for the observed declines of *P. nemoralis* (Section 2). It responds to decreasing light fluxes as a typical shade species: reduced relative growth rate, decreased root weight ratio in favour of above-ground biomass and reduced leaf and stem dry matter content (Corré, 1983). Nevertheless, numerous woodland perennials do require recurrent light phases to maintain viable populations and assure their long-term survival (Jacquemyn, Brys, Honnay, & Hermy, 2008; Van Calster, Endels, Antonio, Verheyen, & Hermy, 2008). *Poa nemoralis* seems no exception. Increasingly, dark woodlands and associated litter accumulation, due to changes in management and dominant canopy species, may still adversely affect *P. nemoralis*, as suggested by the findings of Verheyen et al. (2012), Plue, Van Gils, et al. (2013) and Naaf and Kolk (2015), by limiting both seed production (Plue, De Frenne, et al., 2013) and germination (Eriksson, 1995; Jankowska-Blaszczuk & Daws, 2007; see Section 8). Moreover, Tinya and Ódor (2016) observed that the spatial pattern of *P. nemoralis* abundance in a temperate deciduous woodland in Hungary was congruent with spatial light availability. Kelemen, Mihók, Gálhidy, and Standovár (2012) identified

a similar trend in large canopy gaps (40 m in diameter) in Hungarian beech woodlands. *Poa nemoralis* mostly increased its presence in the central parts of these gaps, where canopy openness was at least 40%. Hence, the species seems to forage actively for light in the woodland understorey, which is beneficial for its survival and necessary for its reproduction.

Poa nemoralis biomass production—without interspecific competition—was highest at a relative illumination of 67% (light fluxes relative to outside the woodland) producing approximately 6 kg/ha but is reduced to only 4.4 and 1.4 kg/ha at 23% and 5% relative illumination, respectively (Eber, 1972).

5.3 | Effect of frost, drought, etc.

Experimentally induced drought stress (7–10 days of drying out the soil at 35°C) reduced soil moisture content beyond the permanent wilting point of 7.7% to 5% and 3%. This resulted in 80% and 35% survival of *P. nemoralis* shoots, respectively, censused 3 weeks after soil moisture levels had been restored to 70%. If plants received nitrogen addition prior to the stress experiment (NH₄SO₄ applied at a rate of 2.3 kg per 92.9 m²), survival dropped to 35% and 15%, respectively. Carroll (1943) offers no mechanistic explanation as to why N addition decreases survival during drought.

In the same study, Carroll (1943) found low survival (<15%) of plants exposed to either 50°C soil or air temperature during a 6-hr period, under normal soil water availability, that is, significantly less compared to other spp. tested, including *Poa pratensis* (40%–80% survival), *P. annua* (40%–60%) and *P. trivialis* (35%–60%). This may be indicative of an adaptation in *P. nemoralis* to the well-buffered, stable microclimatic conditions in the woodland understorey (De Frenne et al., 2019). Soil temperatures down to −10°C had little effect on plant survival (70%–80%), except when plants received nitrogen addition prior to the frost event, in which case survival dropped to 30% for −5°C and to 5% for −10°C. Carroll (1943) suggests that high nitrogen concentrations may interfere with the cold hardening. Soil temperatures of −15°C were lethal for *P. nemoralis*, irrespective of soil nitrogen levels (Carroll, 1943).

As with many other grass species, *P. nemoralis* leaves can be colonized by clavicipitaceous fungal epiphytes, such as *Epichloë typhina* Tul. & C. Tul., which are known to enhance drought tolerance (see Section 9).

6 | STRUCTURE AND PHYSIOLOGY

6.1 | Morphology

Poa nemoralis has sympodial, monocyclic shoots, that is, their life span from sprouting to fruit set occurs within 1 year (Klímešová et al., 2017). Basal branching is mainly extravaginal, with young shoots arising from the base of the leaf sheaths. The leaves have an average life span of 39 days (Ryser & Urbas, 2000). Ryser and Wahl

(2001) found an SLA of $32 \text{ mm}^2/\text{mg}$, a leaf dry matter content of 0.178 g/g and a leaf area ratio (LAR; area of CO_2 assimilating surface per plant dry mass) of $12.8 \text{ m}^2/\text{kg}$. Blondeel et al. (2020) recorded a mean of SLA of $52.5 \pm 1.7 \text{ mm}^2/\text{mg}$ ($\text{PAR} = 7.8 \mu\text{mol s}^{-1} \text{ m}^{-2}$; 45 individuals) and $50.0 \pm 2.3 \text{ mm}^2/\text{mg}$ ($\text{PAR} = 31.8$; 51) in *P. nemoralis* plants grown in experimental mesocosms in Aalmoesene Forest (Belgium). The significantly lower SLA recorded by Ryser and Wahl (2001) is a likely result of *P. nemoralis* individuals being grown in full daylight conditions with a PAR of $48\text{--}56 \mu\text{mol s}^{-1} \text{ m}^{-2}$. Ishtiaq et al. (2018) reported 1–3 rows of paracytic stomata, with two subsidiary cells parallel to the long axis of the pore, on both the adaxial ($25\text{--}31 \mu\text{m}$ long, $9.5\text{--}15 \mu\text{m}$ wide) and abaxial ($13\text{--}27 \mu\text{m}$ long, $17\text{--}19 \mu\text{m}$ wide) intercostal zones of the leaf epidermis. Stomatal density on the upper (adaxial) surface of the leaves is 3.8 (range 3–16) stomata/ mm^2 , while the lower surface has a mean of 118 (range 110–123) stomata/ mm^2 (Fitter & Peat, 1994).

Poa nemoralis has an adventitious root system, with roots forming on the nodes of the epigeogeneous rhizome, eventually replacing the primary root (Figure 4; Klimešová et al., 2017). Based on a comparative study of the root anatomical traits of 19 Central European grass species, Wahl and Ryser (2000) demonstrated that the number of xylem vessels (mean of $3.86 \pm \text{SE } 0.55$) in *P. nemoralis* was comparable to other shade-tolerant grasses such as *Melica nutans* (4.38 ± 0.60), but considerably higher than in shade-intolerant *Poa* species such as *P. pratensis* (1.88 ± 0.23). The inverse was true for the proportion of xylem in the root cross-sectional area ($1.33 \pm 0.15\%$ and $1.33 \pm 0.10\%$ in *P. nemoralis* and *M. nutans*, respectively, vs. $0.62 \pm 0.06\%$ for *P. pratensis*). Other root anatomical characteristics such as root tissue mass density ($0.160 \pm 0.023 \text{ mg/mm}^2$) and root cross-sectional area ($0.164 \pm 0.021 \text{ mm}^2$) were comparable to *P. pratensis*.

6.2 | Mycorrhiza

Arbuscular endomycorrhizal (AM) fungi have been found repeatedly to colonize the roots of *P. nemoralis* (Akhmetzhanova et al., 2012; Göransson, Olsson, Postma, & Falkengren-Grerup, 2008; Harley & Harley, 1987; Hempel et al., 2013; Maier, Hammer, Dammann, Schulz, & Strack, 1997; Väre, Vestberg, & Eurola, 1992; Wang & Qiu, 2006). For instance, Maier et al. (1997) demonstrated that the roots of *P. nemoralis* were associated with the AM fungus *Rhizophagus irregularis* Walker & Schüßler (Division: Glomeromycota; Order: Glomerales). Furthermore, a study by Göransson et al. (2008) in oak woodlands in southern Sweden revealed that the colonization of AM fungi in *P. nemoralis* significantly exceeded fine endophyte (FE) colonization. However, under acidic conditions, both AM and FE fungi showed remarkably low colonization rates, leaving them to conclude that this species likely depends on alternative strategies to cope with nutrient deficiency or aluminium toxicity on acidic woodland soils, rather than mutualism with endophytic fungi.

Poa nemoralis roots are also colonized by the ectomycorrhizal fungus *Tuber aestivum* Vittad. (Division: Ascomycota; Order: Pezizales),

where it forms a non-ectomycorrhizal, auxiliary type of association with this non-host species (Gryndler, Černá, Bukovská, Hřelová, & Jansa, 2014). Microscopic examination of transversal root sections indeed confirmed that fungal hyphae were not present in the volume of the deep root tissues, but suggests that the root-associated mycelium of *T. aestivum* is localized in the decomposing cell layers on the root surface. Although the functional importance of this association remains unknown, the survival of *P. nemoralis* in the midst of a fungal colony suggests that its defences against colonization of its roots (e.g. the production of allelochemicals) are balancing out the colonization activity of the fungus. Alternatively, as deep root tissues are likely not penetrated by the fungus, due to the nature of the non-ectomycorrhizal association as described above, the superficial contact between roots and mycelium is insufficient to activate plant defences, or plant defences are induced but are not manifested as any visible change to root morphology (i.e. no visual plant defence marks, such as tissue necrosis, recorded under microscopic evaluation).

6.3 | Perennation: Reproduction

Poa nemoralis is a hemicryptophyte with good winter hardiness (Gibson, 2009; Shildrick, 1990). While the culms die in autumn, the basal nodes and internodes that make up the epigeogeneous rhizomes remain alive, acting as a bud bank from which new shoots and tillers develop the next spring (Heide, 1986; Klimešová et al., 2017). The bud bank, that is, all buds on the plant body (excluding roots) that can give rise to new shoots (Raunkiaer, 1934), consists on average of c. 10, with c. five buds at the surface and c. five buds below the surface, the latter at a mean depth of 3 cm (Klimešová et al., 2017). Clonal growth occurs by means of tussock fragmentation of the epigeogeneous rhizome (Section 5.1) and is slow, averaging 0.07 m in lateral vegetative spread per year (Klimešová et al., 2017). The species may occasionally form lawns with up to 30 cm long runners (Duwense, 2000).

First-year seedlings may flower readily in response to long days without any preceding exposure to cold temperatures or short-day conditions (Heide, 1994). *Poa nemoralis* will flower annually, though a short photoperiod and cold temperatures may delay flower development and reduce seed set (Heide, 1994).

Poa nemoralis was found to migrate across ancient–recent woodland ecotones in southern Sweden at rates between 0.47 and 10.76 m/year, putting it among the fastest of woodland understorey species (Brunet et al., 2012; Brunet & von Oheimb, 1998). In a 14.5-ha deciduous forest in Central Sweden, Fröborg and Eriksson (1997) similarly established that *P. nemoralis* had the highest colonization rate of 45 understorey species (using inventory data of 132 permanent plots from 1970 and 1993). In light of this combined evidence that the species produces large numbers of seeds and has a mean lateral vegetative spread of only 0.07 m/year, it is fair to assume that reproduction by seed is more important than vegetative reproduction for the spread and survival of the species.

6.4 | Chromosomes

The somatic (2C) nuclear DNA content in a zygotic cell of *P. nemoralis*, measured on Czech material, amounted to 5,160.57 million base pairs, with the percentage of guanine and cytosine bases being c. 47% (Šmarda et al., 2019). The mass of the nuclear DNA in a haploid cell of *P. nemoralis* amounts to 2.75 pg (Leitch, Johnston, Pellicer, Hidalgo, & Bennett, 2019).

Cytological investigations have established seven as the basic chromosomal number of the genus *Poa* (Avdulov, 1931, 1933; Müntzing, 1933; Stählin, 1929). Armstrong (1937), investigating *P. nemoralis* from an English commercial source, found the species to be hexaploid, $2n = 6x = 42$, which seems to be the chromosome number most commonly found among European populations (Stählin, 1929; The Netherlands: Gadella & Kliphuis, 1963; Switzerland: Duckert-Henriod & Favarger, 1987; Czech Republic: Šmarda et al., 2019). Other chromosome numbers have also been reported ($2n = 56$: Müntzing, 1933; $2n = 28$: Patterson, Larson, & Johnson, 2005; $2n = 28, 35$: Kelley, Johnson, Waldron, & Peel, 2009). Varying chromosome number, probably of autopolyploid origin (Armstrong, 1937), occurs in the species and is a probable result of frequent apomictic reproduction recorded in *P. nemoralis* (Naumova, Osadtchiy, Sharma, Dijkhuis, & Ramulu, 1999).

In a phylogenetic study of *Poa* species, nuclear DNA sequences from a tetraploid *P. nemoralis* clustered together with sequences from other *Poa* species rather than with each other (Patterson et al., 2005), suggesting a polyploidization event pre-dating the origin of *P. nemoralis*. Both nuclear and chloroplast markers suggested *P. palustris* to be a sister taxon of *P. nemoralis* (Patterson et al., 2005).

6.5 | Physiological data

Ryser and Wahl (2001) found that Swiss individuals of *P. nemoralis* had a mean net assimilation rate, that is, the rate of total dry mass increase per leaf area and time, of $13.0 \text{ g m}^{-2} \text{ day}^{-1}$ when grown in a high-light environment. In plants with an average relative growth rate of $0.166 \text{ g g}^{-1} \text{ day}^{-1}$ and an average height at maturity of 0.37 m, Wahl and Ryser (2000) found a root tissue mass density of 0.160 mg/mm^3 and a relatively high number of xylem vessels per unit root cross-sectional area (26.2 n/mm^3). Blondeel et al. (2020) recorded leaf N concentration of $4.7 \pm 0.3 \text{ g N/100 g}$ leaf dry mass, measured on eight individuals under 95% forest canopy cover. A root:shoot ratio of 0.7 was found by Falkengren-Grerup, Månsson, and Olsson (2000) when grown at a pH of 4.5. Simultaneously, a mixture of amino acids and methylamine were offered at $100 \text{ } \mu\text{mol/l}$, serving as a source of organic and inorganic nitrogen, respectively. *Poa nemoralis* proved to take up significant quantities of amino acids ($5.8 \pm 0.2 \text{ } \mu\text{mol g}^{-1} \text{ dw root hr}^{-1}$), compared to nine other tested species (mean 4.6; range 1.6–6.3 $\mu\text{mol g}^{-1} \text{ dw root hr}^{-1}$). Uptake of methylamine was relatively high in absolute terms compared to uptake of amino acids (25.2

$\pm 3.1 \text{ } \mu\text{mol g}^{-1} \text{ dw root hr}^{-1}$), but was average when compared to methylamine uptake of nine other species (mean 42.6; range 2.4–175.2 $\mu\text{mol g}^{-1} \text{ dw root hr}^{-1}$). The uptake ratio of amino acids to methylamine was 0.23, compared to a mean of 0.34 (range 0.02–1.42). This ratio establishes capacity of the species to use organic nitrogen as a nitrogen source. Interactions with soil-available nitrate, other inorganic nitrogen, acidity and carbon content suggest that *P. nemoralis* can use organic nitrogen efficiently as a source, even in the presence of large quantities of inorganic nitrogen.

For *P. nemoralis* growing at low inorganic nitrogen concentrations, the potential nitrification in the rhizosphere was similar to that in the bulk soil, although it was higher in the rhizosphere than in bulk soil when nitrogen availability increased in the bulk soil. This suggests that *P. nemoralis* may prefer NO_3^- as a nitrogen source, which is underlined by the observation that the species is more common in the field at higher NO_3^- percentages (Falkengren-Grerup, 1995b; Olsson & Falkengren-Grerup, 2000). In an incubation experiment with soils from over 600 deciduous woodland plots from across southern Sweden, the 369 sites where *P. nemoralis* was recorded had moderately high mineralization rates for both NO_3^- and NH_4^+ , indicating that the species may indeed use both forms of nitrogen (Diekmann & Falkengren-Grerup, 1998). However, the addition of N in equal amounts of NO_3^- and NH_4^+ , at concentrations three to nine times greater than ambient N deposition in southern Sweden, led to a decrease in the cover/biomass of *P. nemoralis* over five successive years. Underlying causes are possibly the accompanying soil acidification resulting in toxic levels of hydrogen and aluminium, a deficit in essential elements with high N concentrations in plant tissues (Falkengren-Grerup, 1993), or uptake of NH_4^+ to toxic levels in plant tissues (Falkengren-Grerup, 1995b). Consequently, the interaction between soil acidity, nitrogen availability and nitrogen form (NH_4^+ or NO_3^-) may be a key factor which controls the distribution of *P. nemoralis*. In very acidic soils, for example, the lack of nitrification may be responsible for the species' low frequency of occurrence (Falkengren-Grerup, 1995b) as without nitrification, NH_4^+ acts as the only available nitrogen source. Falkengren-Grerup and Lakkenborg-Kristensen (1994) did establish experimentally that *P. nemoralis* growth was clearly significantly reduced when only NH_4^+ was offered ($<100 \text{ mg}$ of shoot biomass; both at concentrations of 0.2 and 0.4 mM NH_4^+ , pH = 4.2), compared to offering a mixture of 0.1 mM NO_3^- + 0.1 mM NH_4^+ ($\sim 200 \text{ mg}$ of shoot biomass). However, growth of *P. nemoralis* remained similar when experimentally subjected to either 0.2 mM NH_4^+ or 0.2 mM NO_3^- + 0.2 mM NH_4^+ flow solutions (pH = 4.2: Falkengren-Grerup & Lakkenborg-Kristensen, 1994; pH = 4.5: Falkengren-Grerup, 1995b). This seems to suggest that NH_4^+ may be taken up to a much larger extent than NO_3^- when both are present at sufficiently high concentrations, resulting in a poor growth response as when NH_4^+ is the only N source. The most plausible reason is the uptake of NH_4^+ to potentially toxic tissue levels that inhibit growth. In summary, its complex physiological responses to NH_4^+ and NO_3^- control the species' distribution in response to soil characteristics but also how the species responds to global-change drivers such as acidification and eutrophication.

Poa nemoralis is among the few perennial grasses that flower in response to long-day (LD) conditions alone (Heide, 1994). Cooper and Calder (1964), studying a Welsh population, found no requirements for either short days (SD) or vernalization at low temperatures for the induction of flowering. The species flowered in continuous light in a warm greenhouse. Heide (1986) confirmed in a Norwegian population that first-year seedlings readily flowered without having been exposed to either SD conditions or low temperatures. In a 12-hr photoperiod, individuals remained vegetative for longer than 4.5 months (Heide, 1986). The critical photoperiod was determined to be 14 hr at 15°C and slightly longer at lower temperatures (Heide, 1986). When flower development took place in 12-hr photoperiod, a minimum of two LD cycles was required for floral induction, and at least double that number was needed for flower development in an 8-hr photoperiod (Heide, 1986). SD conditions also strongly decreased seed set (Heide, 1986).

6.6 | Biochemical data

Germinating seeds and seedlings of *P. nemoralis* exude mainly monocarboxylic acids such as formate ($0.13 \pm 0.06 \mu\text{mol/g}$ seeds) and lactate ($0.47 \pm 0.03 \mu\text{mol/g}$ seeds) and to a lesser extent di- and tricarboxylic acids such as citrate ($0.05 \pm 0.02 \mu\text{mol/g}$ seeds) and oxalate ($0.05 \pm 0.02 \mu\text{mol/g}$ seeds). Tyler and Ström (1995) subsequently conclude, based on the low exudation rates of the latter, that the ability of *P. nemoralis* to solubilize and absorb Fe and P from limestone soils is limited, constraining its capacity to colonize limestone soils (pH >8), compared to silicate soils (pH 4–5).

In a greenhouse experiment with potted *P. nemoralis* plants infected with *Epichloë/Neotyphodium* endophytes, no detectable amounts of the protective alkaloids N-formylloline, N-acetylloline, ergovaline or peramine could be found (Leuchtmann, Schmidt, & Bush, 2000). In contrast, colonization by the mycorrhizal fungus *Rhizophagus irregularis* resulted in accumulation of fungus-induced cyclohexenone derivatives (Maier et al., 1997).

7 | PHENOLOGY

Poa nemoralis appears to have a stable first flowering date, suggesting day-length rather than temperature dependence in floral initiation. In Wytham Woods in central England, Fitter, Fitter, Harris, and Williamson (1995) found that the first flowering date of *P. nemoralis* was 19 May (± 2.5 days), based on three decades of phenological observations. Similarly, though only based on 3 years of observation in southern Norway, Heide (1986) found that the first flowering date was 1 or 2 July. This limited dependence on temperature compared to numerous other species in the local flora of Wytham Woods (cf. Fitter et al., 1995) is likely to be because flower induction in *P. nemoralis* depends strongly on long-day induction for a limited number of days (Section 6). Flowering in the British Isles and Germany lasts c. 2 months, with the bulk of flowering spread across June and

July (Fitter & Peat, 1994; Klotz, Kühn, Durka, & Briemle, 2002). Flowering individuals can be found between April and August, and between July and September, in the southern and northern parts of its Eurasian range, respectively (Iberian Peninsula: Ortega-Olivencia & Devesa, 2018; Scandinavia: Mossberg & Stenberg, 2018), with this phenological variation likely representing the latitudinal, seasonal change in photoperiod. Under long-day induction, flowering can still be significantly delayed at low temperatures, from 27.1 days at 18°C for floral development to 77.0 days at 6°C (Heide, 1986).

Seeds are ripe by the end of June in southern England, while harvesting of ripe seeds of *P. nemoralis* along a latitudinal gradient from N. France to Norway occurred between 1 July (Ghent, Belgium) and 19 August (Trondheim, Norway), with the mean collection date being 17 July (Plue, De Frenne, et al., 2013). Seeds are likely dispersed once mature, as they were found in fresh red deer pellets in increasing numbers in July (3 seeds per 200 g dry dung) and August (7 seeds) in Slovenia (Steyaert, Bokdam, Braakhekke, & Findo, 2009). Moreover, after endozoochorous dispersal, germination may be immediate and successful under favourable conditions (Section 8), as investigations of European bison faeces in Białowieża forest (Poland) found a juvenile *P. nemoralis* individual on bison faeces as early as August (Jaroszewicz, Pirożnikow, & Sagehorn, 2008). Seedlings start appearing within 5 days after sowing, without the need for stratification (Heide, 1986), with at least 70% of seeds germinated within less than 30 days (Olsson & Kellner, 2002).

Ryser and Urbas (2000) found the leaves of *P. nemoralis* to have an average life span of 39 days in their experiments. Remarkably, no new leaves were formed by the species in the weeks after 26 July, in contrast to all 31 other studied grass species.

8 | FLORAL AND SEED CHARACTERS

8.1 | Floral biology

The number of florets per spikelet in *P. nemoralis* varies with plant age and shade (Sinclair, 1826). When grown in light conditions from seed, young individuals form three to five florets per spikelet, increasing up to even nine florets as plants age. Under shaded conditions, *P. nemoralis* may only contain one to three florets per spikelet.

Based on flow cytometry analysis of a suite of *P. nemoralis* seeds, Kelley et al. (2009) concluded that 17 batches of 50 seeds (from seven different accessions) resulted from pseudogamous apomictic reproduction (2 and 5 C peaks during flow cytometry). Another two batches of 50 seeds from a single accession revealed seeds produced via facultative apomixis (2, 3 and 5 C peaks; Kelley et al., 2009), that is, both sexual and vegetative reproductive modes were present among the various individual mother plants of those seed batches. It can hence be deduced that apomixis may be a frequent means of reproduction in *P. nemoralis*. However, the environment (e.g. photoperiod) may be important in exercising control over the dominant reproduction mode in *Poa* spp., affecting apomixis frequencies (Kelley et al., 2009).

Apomixis in *P. nemoralis* is pseudogamous diplospory (Connor, 1979). A megagametophyte is formed from a cell in the archesporium, and contains an egg cell that will develop into an embryo through parthenogenesis, the latter process occurring before anthesis (Naumova et al., 1999). Fertilization of the megagametophyte is required to ensure that an endosperm is formed (hence pseudogamy), yet is likely uncommon, as the frequent lack of an endosperm is responsible for low production of viable seeds (Naumova et al., 1999).

Sexual reproduction in *P. nemoralis* involves a mixed-mating system. It is pollinated by wind, releasing its pollen between 5 and 8 p.m. (Gibson, 2009), and has also been reported to be self-compatible (Klotz et al., 2002). About 36% of *P. nemoralis* pollen germinated when applied to stigmas at room temperature, and observed after 4 hr of incubation (Lausser, 2012).

Vivipary was also reported in *P. nemoralis* by Heide (1986), who described the phenomenon as 'not normal'. As an obligate single-induction species, which only depends on long-day conditions for flower induction, complete induction triggers seminiferous reproduction in 95.1%–98.7% of spikelets, with no vivipary, irrespective of temperature. Short days (10 hr) after insufficient long-day induction, however, trigger viviparous proliferation of inflorescences (23.8%–33.4%), though seminiferous spikelets develop as well (14.1%–39.0%). Moreover, declining temperatures significantly reinforce this effect, with 33.4% versus 23.8% of spikelets being viviparous at 12 and 21°C ($n = 10$ individuals per treatment), respectively. Vivipary is hence probably a result of incomplete floral induction producing insufficient concentrations of flowering hormone(s). Consequently, vivipary is likely to occur increasingly in *P. nemoralis* when photoperiod and temperature decrease towards the end of the growing season (Heide, 1994).

8.2 | Hybrids

No hybrids of *Poa nemoralis* are currently known from the British Isles. *Poa* specimens collected from a mixed population of *Poa chaixii* (a non-native species) and *P. nemoralis* in West Norfolk in 1972 were at first determined to be a hybrid of the two species by C.E. Hubbard (Libbey & Swann, 1973), but were later identified to be fertile, weak and slender individuals of *P. chaixii* (R.P. Libbey & C.A. Stace, unpubl. data).

However, it is possible that hybrids of *P. nemoralis* exist, yet remain unrecorded. On the one hand, that may be due to its taxonomic complexity. The many cytological races and hybrid polyploid populations with variable morphology may be generalized into agamosperous complexes of unclear taxonomic status. However, morphological continuity indicates that they can successfully reproduce sexually as well, and their reproductive hybrids form mixed seed-producing populations with parent *P. nemoralis* races (Mezina, Bayahmetov, Feoktistov, & Olonova, 2016; Olonova, 2007). On the other hand, *P. nemoralis* is a suspected basal ancestor of species in the *Stenopoa* section (a group of c. 40, mostly Eurasian *Poa* spp. including *P. glauca*,

P. palustris, *P. compressa* and *P. angustifolia*) and reticulate hybridization among these species probably occurred during the Pleistocene migration (Mezina et al., 2016; Olonova, 2007; Soreng, 1990). Within the *Stenopoa* section, hybridization is reportedly easy and many member species have formed morphologically and genetically distinct hybrid populations. If and when stabilization by apomixis occurs, this may give rise to new (sub)species with their own ecological niche. For example, *Poa nemoralis* subsp. *lapponica* (Prokudin) Tzvelev is a suspected ancient hybrid of *P. nemoralis* and *P. palustris* that arose during the last glacial period (Guanghua, Liang, Soreng, & Olonova, 2006; Olonova, 2007), separated ecologically from its ancestors by growing on open stony, rocky and grassy slopes and alpine meadows. Recent *Poa* hybrids may remain difficult to isolate and identify given continuity and overlapping variability in morphological characteristics (Mezina et al., 2016; Olonova, 2007; Patterson et al., 2005; Soreng, 1990). Taxonomic complexity is exacerbated by the similarly uncertain taxonomic status of the many cytological races in other *Stenopoa* members, such as *P. glauca* and *P. palustris*, with which *P. nemoralis* may hybridize. Moreover, introgressive hybridization is common and intermediates between *P. nemoralis* and other *Poa* species are common where they are sympatric and the genetic heterogeneity of these populations is retained through apomixis (Gillespie & Boles, 2001; Mezina et al., 2016; Olonova, 2007). This is supported by morphological studies in Siberia, where hybrids between *P. palustris* and *P. nemoralis* are more similar to *P. palustris* (Mezina et al., 2016; Olonova, 2007). Hybrids between *P. palustris* and *P. nemoralis* are also common in northern Scandinavia (Mossberg & Stenberg, 2018).

Despite these taxonomic difficulties, a number of recent hybrids are known and could potentially be found in the British Isles, as the hybridization partner is present. Recent hybrids of *P. nemoralis* and *P. palustris* are treated as *P. × intricata* Wein and are known to occur in Kazakhstan, southern Siberia and northern Eurasia (including Scandinavia). Other known European hybrids potentially present on the British Isles include *P. compressa* × *P. nemoralis* (*P. × figertii* Gerhardt, recorded in Sweden, Austria, Germany, France) and *P. glauca* × *P. nemoralis* (Central-Sweden). In the colder, northwestern, mountainous parts of Britain (and in northern Scandinavia), *P. nemoralis* co-occurs with *P. glauca*, and the boundary between montane forms of non-glaucous *P. glauca* and *P. nemoralis* is reportedly vague, possibly due to hybridizations, although these forms are sometimes grouped as the separate species '*P. balfourii*' (Trist, 1986). There are also ecological contrasts between the known hybrids. Putative hybrids between *P. nemoralis* and *P. palustris* are common in flood valleys and lowlands, whereas hybrids between *P. nemoralis* and *P. compressa* are common on shallow, dry soil in woodland margins. Hybrids between *P. nemoralis* and *P. glauca* occur mostly in mountain and subarctic valleys and in low-alpine and low-arctic thickets (Olonova, 2007).

8.3 | Seed production and dispersal

Poa nemoralis produces large numbers of caryopses (hereafter referred to as seeds), which are small (1.5 mm × 0.4 mm) and light

(mean air-dry mass 0.2 mg; range 0.12–0.25, $n = 1,000$; Royal Botanical Gardens Kew, 2019). Across N.W. Europe, based on seed counts from 20 inflorescences in five populations from seven European countries, the species produced a mean of 58.9 ($SE \pm 33.9$; range 13–368) seeds per inflorescence (Plue, De Frenne, et al., 2013), both sexually and/or via apomixis (Naumova et al., 1999). Lack of an endosperm in apomictic seeds may lead to seed degeneration and death, resulting in as little as 17.5%–31.6% of seeds being viable (based on seeds of 1,000 flowers on two Russian populations; Naumova et al., 1999). Inflorescences from an area of 4 m² produced 17,801 seeds (range: 7–84,656). Seed production did not vary in response to climatic variables such as mean annual temperature, growing degree-days or temperature range (Figure 5), nor in response to pH, soil moisture or latitude. However, seed production did increase as populations grew larger (Figure 5). Moreover, Plue, De Frenne, et al. (2013) discovered an additive, negative affect of increasing overstorey canopy cover to that of population size, implying that populations growing in more shaded conditions produced significantly fewer seeds (Figure 5).

The weakly bristly diaspores of *Poa nemoralis* are generally considered as having limited adaptations to facilitate long-distance dispersal

by biotic or abiotic vectors. Consequently, it has been assumed that the majority of seeds are deposited near their maternal plant (barochory). However, even barochorous species can be actively dispersed by animals (Couvreur, Couvreur, Vandenberghe, Verheyen, & Hermy, 2004). The diaspores have been reported by numerous studies to disperse via epizoochory, that is, adhering to the fur of animals such as wild boar (*Sus scrofa* L.) and dogs (*Canis lupus familiaris* L.; Graae, 2002; Heinken & Raudnitschka, 2002). *Poa nemoralis* was the third most abundant seed present in the fur and hooves of wild boar in Brieselang forest (Germany). They made up some 15.9% (441 seeds) of all seeds found on nine wild boars sampled, while the other 36 species on average accounted for 2.34% each (range <0.1%–21.8%; Heinken & Raudnitschka, 2002). Hence, wild boar is a potent long-distance dispersal vector for *P. nemoralis*, given its significant home range (100–700 ha, minimum diameter of 1.1–3 km; Heinken & Raudnitschka, 2002). Endozoochory has also been reported in *P. nemoralis*, with seeds being dispersed in the dung of European bison (*Bison bonasus* L.; Jaroszewicz et al., 2008) and red deer (*Cervus elaphus* L.; Steyaert et al., 2009). Jaroszewicz et al. (2008) found a total of 84 juvenile, vegetative and regenerative *P. nemoralis* individuals growing on 114 bison dung piles (1,437 seeds of confirmed endozoochorous origin; 6.24% being *P. nemoralis*). Moreover, *P. nemoralis* had previously not been recorded in the study area, supporting

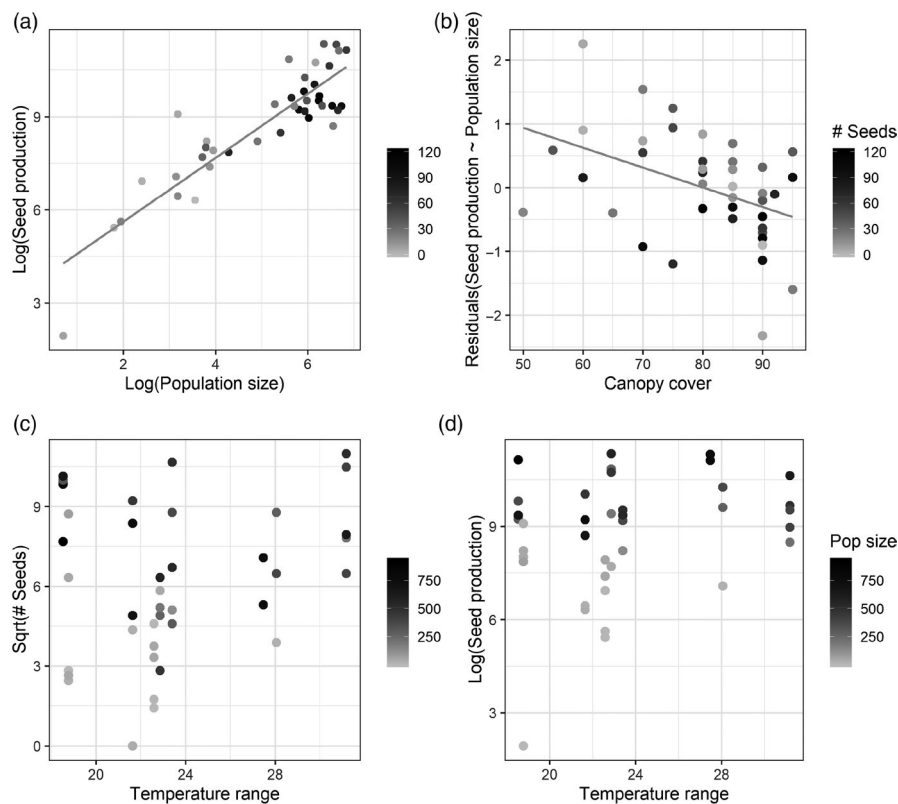


FIGURE 5 Total seed production and seed bank size in 2 m × 2 m plots within stands of *Poa nemoralis*, in relation to population size, canopy cover and temperature range on an environmental gradient across N.W. Europe. (a) Relationship between total seed production and population size; (b) residual relationship between total seed production and canopy cover after accounting for population size; (c) relationship between seed bank size (#Seeds) and annual temperature range; (d) relationship between seed production and annual temperature range. Regression lines indicate significant relationships. Population size was approximated by the number of inflorescences. The greyscale gradient of points represents increasing seed bank size (a, b) or increasing population size (c, d). Data are derived from Plue, De Frenne, et al. (2013)

the long-distance dispersal potential of endozoochory. Steyaert et al. (2009) recorded 10 *P. nemoralis* seeds among 1,766 seeds per 200 g dry red deer dung. Moreover, radio-collar telemetry suggested that red deer could thus support potential endozoochorous dispersal distances up to 4,853 m (Steyaert et al., 2009).

Seeds can remain buoyant in water for half a day (Andersson, Nilsson, & Johansson, 2000) and, in woodland streams prone to flash flooding, the species seems to exploit this capability (Araujo-Calçada et al., 2015; Skoglund, 1990). Araujo-Calçada et al. (2015) found seeds of *P. nemoralis* being deposited by the hydrochorous seed rain in the riparian zone of woodland metacommunities in northern France. Seeds were deposited by flash flooding in 15 out of 54 seed rain plots (28%), whereas the species occurred along the riparian zone in 23 out of 92 plots (25%).

Temporal dispersal by means of persistent soil seed banks may also be considerable in *P. nemoralis*. It has indeed been found in the persistent soil seed bank of ancient (neglected) hazel coppice woods and young oak–beech plantations in Essex, Suffolk, Hampshire and Dorset (Brown & Oosterhuis, 1981; Buckley, Howell, & Anderson, 1997), reaching a mean seed density of 17 seeds/m² (Buckley et al., 1997). This figure is considerably lower than densities reported from across N.W.-Europe ranging between 55 and 169 seeds/m² (Bossuyt & Hermy, 2001; Plue, Thompson, Verheyen, & Hermy, 2012). These lower densities may be due to the potentially darker conditions in the woodland understorey (neglected coppices and young plantations) which lowers seed production (Plue, De Frenne, et al., 2013) and/or increases net seed mortality due to seed senescence. Targeted seed bank sampling within established *P. nemoralis* populations, however, returned an average seed density of 3,992 seeds/m² (Plue, De Frenne, et al., 2013). Although populations were sampled across a latitudinal gradient from northern France to Norway, seed bank densities of *P. nemoralis* were only affected by population size (i.e. total potential seed production) with no impact of soil pH, moisture, light conditions in the woodland understory or climate variables (Figure 5; Plue, De Frenne, et al., 2013). *Poa nemoralis* possessed a relatively high seed accumulation index of 0.15 compared to, for instance, 0.07 in *Milium effusum* (Plue, De Frenne, et al., 2013), meaning that the species occurred in the seed bank without being present in the vegetation in 15 out of 100 plots. The latter pattern, combined with the observation of in situ emergence of *P. nemoralis* seedlings in plots where adult plants were absent but seeds were banked below-ground (Eriksson, 1995), leads to the conclusion that *P. nemoralis* does form a long-term persistent soil seed bank.

8.4 | Viability of seeds: Germination

Under open storage in temperate conditions, germination success of *Poa nemoralis* is reduced by 50% after 3.8 years (Priestley, 1986). Seeds withstand long-term storage (air-tight containers, with seed moisture content between 3% and 7% at –18°C or lower); at the Millennium Seed Bank of The Royal Botanical Gardens Kew, germination remained at 90%–92.5% after 13 years of storage. Seeds

supposedly lack physiological dormancy, as seeds exposed to a chilling treatment (2°C for 3.5 months) did not germinate markedly better. This suggests that seeds are readily germinable whenever conditions are suitable (Ten Brink, Hendriksma, & Bruun, 2012), although physical dormancy has also been reported (Tiansawat & Dalling, 2013).

Seeds of *P. nemoralis* sown on 1% agar plates reached 69% germination under conditions of alternating 12-hr light at 23°C/12-hr darkness at 9°C over 56 days, increasing to 100% when a 101 mg/L potassium nitrate solution was added to the germination medium (RBG Kew). Germination of seeds collected in Białowieża forest (Poland) increased from no germination to about half of the seeds germinating when the red:far-red light ratio increased (1% agar, 12-hr light/12-hr darkness, 15°C; Jankowska-Blaszczuk & Daws, 2007). This suggests that the small seeds of *P. nemoralis* require light for germination (Jankowska-Blaszczuk & Daws, 2007; Stebler, 1881). Ten Brink et al. (2012) confirmed that seeds of *P. nemoralis* from populations in southern Sweden did germinate better, not only in response to light but also to fluctuating temperatures (both 15°C/5°C and 25°C/15°C treatments; see also Jönsson, 1893). This implies that germination cueing may be a depth-, litter- or gap-sensing mechanism, reducing the chances of failed establishment in small-seeded species such as *P. nemoralis* (Milberg, Andersson, & Thompson, 2000). In situ litter removal in deciduous woodland plots in southern Sweden did indeed dramatically increase the germination of *P. nemoralis*, and no seedlings were found in plots where litter remained present during the experiment (Eriksson, 1995). Germination cueing in *P. nemoralis* has seemingly developed as a means of habitat specialization, allowing the species to adapt to its wooded environment compared to its congeners of open grassland environments (Ten Brink et al., 2012).

Soil chemistry (pH, NH₄⁺, NO₃⁻, P and K) had no apparent impact on the in-situ germination of *P. nemoralis* (Eriksson, 1995). This was reaffirmed by a pot experiment on a mor/moder humus substrate (pH 4.34 ± 0.26, 17-hr light/7-hr darkness, 14–28°C), where neither liming (dolomite) nor acidification treatments (H₂SO₃ or S) affected germination of *P. nemoralis* from Swedish populations, that reached 70%–85% after 30 days (Olsson & Kellner, 2002). Soil moisture does, however, seem to exert control over germination of *P. nemoralis*. In German populations, Donath and Eckstein (2008) reported that continuously humid soil (watered 2–3 times per week) yielded twice as much germination (60%) compared to soil which was watered once a week and which intermittently dried out. However, an increase in germination was observed in *P. nemoralis* in the intermittently dry pots when oak litter was applied (Donath & Eckstein, 2008), suggesting that the litter layer keeps the soil more humid, improving conditions for germination. This again suggests some level of adaptation in *P. nemoralis* to its wooded environment.

8.5 | Seedling morphology

Germination in *P. nemoralis* is epigeal. The emerging coleoptile is between 4 and 6 mm tall, rather tight and colourless. The first

FIGURE 6 Seedling germination of *Poa nemoralis* with bare caryopsis and seedlings at early stages after initial radicle emergence. Seeds germinated on filter paper in Petri dishes kept moist with distilled water, in a climate chamber at 8-hr light at 25°C/16-hr darkness at 10°C. Seedling photographs were taken 13 days after sowing. White squares represent a 500 µm scale. Seeds were made available from accession 135838 from the Kew Millennium seed bank. Photos by Sanne Govaert [Colour figure can be viewed at wileyonlinelibrary.com]



seedling leaf is flat, with a narrow lamina, three-nerved and glabrous (Figure 6; Müller, 1978; Watson & Dallwitz, 1992).

9 | HERBIVORY AND DISEASE

9.1 | Animal feeders or parasites

9.1.1 | Mammals and insect feeders

Several large mammal species feed on *P. nemoralis*. It has been reported as highly palatable to red deer (Steyaert et al., 2009), comprising >10% of the diet during at least one season (Gebert & Verheyden-Tixier, 2001). It was also part of red deer diet in Slovakia, where the investigation of fresh faecal pellets of red deer contained seeds of *P. nemoralis* in July and August.

Graminoids form only a small fraction of the diet of roe deer (*Capreolus capreolus* L.) in Britain, amounting to c. 4%–6% throughout the year (New Forest, Hampshire: Jackson, 1980; Dorset: Hosey, 1981). Graminoids were eaten by 70% of roe deer sampled by Jackson (1980). Although we found no evidence of *P. nemoralis* being consumed by roe deer in the British Isles, Siuda, Zurowski, and Siuda (1969) reported that *P. nemoralis* accounts for 0.4% of the plant volume eaten in spring and 0.1% in winter in Poland.

The review by Schley and Roper (2003) on the diet of wild boar in Western Europe suggests that the importance of *P. nemoralis* as a food source is limited. They identified only Janda (1958) as reporting it as a part of the wild boar diet, as revealed by the stomach analysis of 24 animals. In the Białowieża forest in Poland, European bison feed on *P. nemoralis*, based on the emergence of *P. nemoralis* seedlings on bison dung (Jaroszewicz et al., 2008). No damage to *P. nemoralis* populations

by these feeding actions was recorded, as would be expected since it is a minority food source for these large animals. *Poa nemoralis* has been reported as possessing 'fine succulent herbage' for sheep grazing in Britain rendering it excellent to be mixed with other grasses sown in shaded woodlands (Moore, 1850).

Smaller mammals also feed on *P. nemoralis*. In a study of year-round food preferences in yellow-necked mice (*Apodemus flavicollis* Melchior) and bank voles (*Myodes glareolus* Schreber) in a temperate deciduous woodland in Poland (Gorecki & Gebczyncka, 1963), both species consumed *P. nemoralis* when it was offered in abundance in a mixture with other woodland herbs. However, although *P. nemoralis* was most abundant in the woodland understorey during spring-summer relative to other woodland herbs, it was clearly less preferred for consumption by bank voles, being eaten on only 10% of the times it was offered (mean and range for other forest herbs: 74%, 60%–90%). It formed a more pronounced part of the diet of yellow-necked mice, being consumed 30% of the times it was offered (mean and range for other woodland herbs: 43%, 10%–80%). Both species occur in the British Isles, with bank vole being widely distributed in wooded habitats, whereas yellow-necked mice are restricted to ancient woodlands in southern England, southern Wales and parts of the Midlands. In Canada, the meadow vole (*Microtus pennsylvanicus* Ord.) has a clear dietary preference for *Poa* spp., and *P. nemoralis* in particular (Bergeron & Juillet, 1979). The species appeared more frequently in the stomach content than in their habitat, based on the stomach-content analysis of 252 meadow voles.

Poa nemoralis is eaten by larvae of several insects, mostly moths (Noctuidae), butterflies (Nymphalidae) and gall flies (Mayetiola). A list of insect feeders is given in Table 1. Leaf mining is recorded for larvae of two Agromyzidae species and one species of Elachistidae. Larvae of several gall fly species produce galls on the stems and roots

TABLE 1 Phytophagous insects on *Poa nemoralis*, their family, life stage that is phytophagous, specific feeding types and plant parts predated, as well as their distribution

Family	Species	Phytophagous life stage	Feeding type	Plant parts	Distribution	References (species; distribution)
Agromyzidae	<i>Phytomyza milii</i> Kaltenbach	Larvae	Mining	Leaves	Europe and UK	1; 2, 3, 4
	<i>Phytomyza nigra</i> Meigen	Larvae	Mining	Leaves	Europe and UK	1; 2, 3, 4
Cecidomyiidae	<i>Mayetiola radicifica</i> (Rubsaaamen)	Larvae	Galling	Roots, stems	NA	5
	<i>Mayetiola graminis</i> (Fourcroy)	Larvae	Galling, gregarious	Roots, stems	Europe	5, 6, 7; 8
	<i>Mayetiola joannisi</i> Kieffer	Larvae	Galling, gregarious	Stems	Europe	5, 6, 7; 8
	<i>Mayetiola poae</i> (Bosc)	Larvae	Galling, gregarious	Roots, stems	Europe	5, 6, 7, 9; 8
Elachistidae	<i>Elachista apicipunctella</i> Stainton	Larvae	Mining	Leaves	Europe and UK	10, 11; 3, 4
	<i>Elachista bifasciella</i> Treitschke	Larvae	Mining	Leaves	Europe (UK absent)	12
	<i>Elachista exactella</i> Herrich-Schäffer	Larvae	Mining	Leaves	Europe (UK absent)	12
	<i>Elachista freyerella</i> Hübner	Larvae	Mining	Leaves	Europe and UK	12
Mindaridae	<i>Anoecia nemoralis</i> Börner	Unspecified	Ant attended	Roots	Europe	13; 8
Nymphalidae	<i>Coenonympha pamphilus</i> (L.)	Larvae			Europe and UK	14, 15; 3, 4
	<i>Pararge aegeria</i> (L.)	Larvae			Europe and UK	14, 16; 3, 4
	<i>Lopinga achine</i> Scopoli	Larvae			Europe	
Noctuidae	<i>Apamea furva</i> (Denis & Schiffermuller)	Larvae		Roots, stems	Europe and UK	14; 3, 4
	<i>Apamea furva</i> (Denis & Schiffermuller) ssp. <i>britannica</i> Cockayne	Larvae		Roots, stems	UK	17, 18; 3, 4
	<i>Apamea scolopacina</i> (Esper)	Larvae	Boring	Flowers, leaves, stems	Europe and UK	17, 18; 3, 4
	<i>Mythimna ferrago</i> (F.)	Larvae			Europe and UK	14; 3, 4
	<i>Mythimna turca</i> (L.)	Larvae			Europe; England and Wales	14, 17, 18; 3, 4
	<i>Pachetra sagittigera</i> (Hufnagel)	Larvae			Europe and south England	14; 3, 4
	<i>Pachetra sagittigera</i> (Hufnagel) ssp. <i>britannica</i> Turner	Larvae			South England	17; 4

Notes: 1. Griffiths (1980), 2. Spencer (1972), 3. NBN Atlas (2017), 4. GBIF (2019), 5. Buhr (1965), 6. Barnes (1946), 7. Ertel (1975), 8. DBIF (2007), 9. Hesse (1969), 10. Steuer (1976), 11. Emmet (1996), 12. Unger (2019), 13. Borner (1952), 14. Allan (1949), 15. Howarth (1973), 16. Blab and Kudrna (1982), 17. Heath and Emmet (1983), 18. Waring and Townsend (2017).

of *P. nemoralis*. Seven species of moths and three species of butterflies have phytophagous larvae on *P. nemoralis*, especially larvae of the moth *Apamea scolopacina* Esper which bore into flowers, leaves and stems. *Lopinga achine* Scopoli (absent from the British Isles) and *Pararge aegeria* L. (common in the British Isles) are both butterfly species which can use *P. nemoralis* as host for its larval stage, though it is less preferred compared to the main host species: *Carex montana* in *Lopinga achine* in south Sweden (Bergman, 2000); and *Brachypodium sylvaticum* in *Pararge aegeria* in England (Shreeve, 1986). Feeding on *P. nemoralis* also led to lower survival of the adults of *Lopinga achine* in the Swedish study. One subterranean aphid species is recorded to be

phytophagous, by infesting the roots of *P. nemoralis*: *Anoecia nemoralis* Börner. This aphid is myrmecophilous, with ants attending the aphids during the subterranean part of their life cycle (Paul, 1977).

9.2 | Plant parasites and diseases

9.2.1 | Fungal parasites

Several parasitic fungi have been recorded in association with *Poa nemoralis*: *Puccinia brachypodii* var. *poae-nemoralis* Cummins & H.C.

Greene, *Uromyces dactylidis* G.H. Otth, *Puccinia poarum* Nielsen and *Uredo* sp. (all Basidiomycota, Pucciniales; Kranz & Brandeburger, 1981). These four species cause a rust disease on the leaves. *Puccinia brachypodii* var. *poae-nemoralis* is abundant in the UK, whereas *Puccinia poarum* and *Uromyces dactylidis* are abundant in the UK and continental Europe. *Uredo* sp. is present more globally but not very abundant in Europe. These fungi are not restricted to *P. nemoralis* as host species, and in turn they may be parasitized by the mycoparasite *Eudarlucia caricis* O.E. Erikss. (Ascomycota, Pleosporales; Kranz & Brandeburger, 1981). Two additional fungi have been found on *P. nemoralis* in Finland, *Telimenella gangraena* Petr. (Ascomycota, Phyllachorales) and *Septogonium oxysporum* Bommer, Rousseau & Sacc. (Ascomycota, 'incertae sedis'), but their importance appears to be negligible (Mäkelä & Koponen, 1976).

9.2.2 | Endophytic fungi

The fungus *Epichloë typhina* (Clavicipitaceae) is recorded in *P. nemoralis*. This fungus lives in symbiosis with several grasses, in an association that ranges from mutualism to antagonism. The fungus lives endophytically, forming hyphae in between leaf cells of the host plant. In the mutualistic form, the fungus is vertically transmitted through infection of the seeds. In the antagonistic form, the fungus forms a mycelium surrounding the flag leaf of developing inflorescences and suppresses seed setting. This situation is called 'choke disease' since the flowering tillers of the host plant are 'choked' (Kirby, 1961; Leuchtman, 2003; Schardl, Leuchtman, & Spiering, 2004). Both mutualistic and antagonistic forms are recorded for *P. nemoralis* (Leuchtman, 2003; Moon, Scott, Schardl, & Christensen, 2000). In addition, it has been shown that endophyte-infected grasses contain alkaloids that protect them from grazing herbivores (Moon et al., 2000; White & Bultman, 1987). However, this does not seem to be the case when *P. nemoralis* is infected by *E. typhina* (Leuchtman et al., 2000; Section 6). White and Cole (1986) studied herbarium collections of several *Poa* species to record the presence of endophytic fungi and did not find endophytes in *P. nemoralis*. This might indicate a lower abundance of the fungus in *P. nemoralis* compared to other *Poa* species such as *P. palustris* and *P. autumnalis*.

Epichloë typhina subsp. *poae* is a member of the *E. typhina* complex that can infect *P. nemoralis*, as well as *P. pratensis* (Europe), *P. secunda* subsp. *juncifolia* and *P. sylvestris* (North America; Leuchtman, Bacon, Schardl, White, & Tadych, 2014). Nevertheless, despite the large size of the *E. typhina* complex (including subspecies and varieties), Schirrmann and Leuchtman (2015) convincingly proved host specificity in *Epichloë typhina* subsp. *poae*, using *P. nemoralis* as study species (Schirrmann & Leuchtman, 2015). Crosses with other members of the *E. typhina* complex infecting *Dactylis glomerata* (*E. typhina*), *Holcus lanatus* (*E. typhina* subsp. *clarkii*) and *Poa trivialis* (*E. typhina*), respectively, showed clear host specificity by the apparent existence of reproductive barriers. This suggests speciation of *E. typhina* subsp. *poae*

in Swiss populations of *P. nemoralis*. Interestingly, the fungus is not only capable of horizontal transmission by infecting host leaves via air-borne spores, but vertical transmission from a mother plant to its offspring has been recorded in *P. nemoralis*, that is, via infected seeds (Leuchtman et al., 2014).

9.2.3 | Bacterial wilt

Bacterial wilt disease can occur on *P. nemoralis*, causing shoots to wilt and become chlorotic; later necrotic stripes appear along the leaves. *Poa nemoralis* holds an intermediate position in susceptibility compared to other *Poa* species, with *P. trivialis* being highly susceptible and *P. pratensis* being practically resistant (Egli & Schmidt, 1982).

10 | HISTORY

There is evidence that *P. nemoralis* was first discovered in Britain by Tilleman Bobart of Oxford and reported by Ray (1696) as *Gramen pratense paniculatum majus angustiore folio* C.B. (Pearman, 2017). However, this early record was initially overlooked and Hudson's (1762) record of *P. nemoralis* ('in sylvis et umbrosis') was taken as the first British record. The current binomial name was coined in Linnaeus *Species Plantarum* in 1753. Evidence for post-glacial occurrence is usually lacking for grasses, including *P. nemoralis*, since pollen analysis does not permit species identification. However, there are numerous sources evidencing macrofossils beginning with the Early Bronze Age (Czech Republic; Bieniek & Pokorný, 2005), continuing through the Early Iron Age (Sweden: Jensen, 1987; Denmark: Helbæk, 2017) up to the Early Middle Ages (Georgia: Kvavadso, Rukhadze, Nikolaishvili, & Mumladze, 2008; Switzerland: Akeret & Kühn, 2008). The discovery of *P. nemoralis* seeds in the stomach of an early Iron Age man in Denmark is remarkable, suggesting the grass to have been part of the human diet at that time (Helbæk, 2017).

There are also clear indications that *P. nemoralis* was part of a group of other grass-like species (e.g. *Luzula luzuloides*, *Milium effusum*, *Poa chaixii*) that have been sown in parkland under trees in Scotland and elsewhere (Ronse & Braithwaite, 2012), although the species is native in surrounding woodlands. These species have referred to as wood lawn neophytes (Ronse & Leten, 2011), that is, an interpreted translation of the German 'Grassameneinkömmlinge' (Hylander, 1943). The practice of sowing grass species into parklands is also known from Sweden (Hylander, 1943). The use of such grass-seed mixtures was characteristic in English landscape gardening which required a grassland cover under trees. In Scandinavia, the introduction of this practice coincided with the introduction of the English landscape style (Ronse & Braithwaite, 2012). Beyond parks and gardens, the grass was also sown in woodlands, in clearings, as well as playing fields, due to its ornamental value as a lawn or turfgrass (Hubbard, 1984; Moore, 1850). The latter possibly led to the species being introduced outside its native range as early as the

1800s. It was imported from the British Isles in grass-seed mixtures for permanent pastures in New Zealand in 1870 (Thomson, 1922), with the earliest records in 1875 in Australia and 1878 in New Zealand (The Australasian Virtual Herbarium, 2015).

11 | CONSERVATION AND MANAGEMENT

Poa nemoralis is common in its wide, native Eurasian range, as well as being naturalized in many parts of the Americas and in the southern hemisphere. Hence, it is of no conservation concern today or in the near future and it is not listed as threatened, endangered or vulnerable in any Red Lists, including those for the British Isles (Cheffings & Farrell, 2005; Dines, 2008; Stroth et al., 2014; Wyse Jackson et al., 2016). Across N.W. Europe, however, the frequency of occurrence of the species in resurveyed semi-permanent plots in ancient woodlands has declined by 3.8%–5.4% (De Frenne et al., 2013; Verheyen et al., 2012). Still, at rank 23, the species is among the top 50 most recorded species in ancient woodlands across Europe, including the British Isles (De Frenne et al., 2013).

Poa nemoralis is considered an indicator species of ancient woodlands across large parts of Europe in its native range—but not German uplands, mountains and Alps, Luxemburg, Czech Republic and Denmark (Heinken, 2019). This includes the British Isles (Kirby, 2006; Rose, 1999), for which Kimberley, Blackburn, Whyatt, Kirby, and Smart (2013) conclude that the species does possess the trait syndromes typical of ancient woodland species (as defined by Hermy, Honnay, Firbank, Grashof-Bokdam, & Lawesson, 1999; Verheyen, Honnay, Motzkin, Hermy, & Foster, 2003). However, expert-based species lists conclude that *P. nemoralis* is not an ancient woodland indicator in Lincolnshire, Derbyshire, Dorset and North Yorkshire (Kirby, 2006; Peterken, 1976) but compare Peterken and Game (1984) for Lincolnshire. Because the species can occur in remnant wooded habitats such as hedgerows (see Section 2) and because of its widespread distribution, the species does not require targeted conservation action. Still, the conservation of ancient woodland habitats (currently only 2% of the surface area of the UK, according to the Woodland Trust) will likely be important in the long-term conservation of the species. *Poa nemoralis* may experience a significant increase in the likelihood of local extinctions if ancient woodland cover is reduced further (Rueda et al., 2015). Given the suite of modern threats to ancient woodlands, including continued destruction (Rackham, 2008), there is an urgent need for increased conservation and protection efforts, which have generally increased too slowly (Watson et al., 2016) for such biodiverse habitats as ancient woodlands.

P. nemoralis is usually also widespread in its introduced range in, for example, North America and it is likely that it is under-reported, as its morphological variation can hinder separation from other common *Poa* spp. (Section 8). Where it has been naturalized, it occupies different types of woodlands, disturbed sites, cattle grazing and wet areas (Dibble, Zouhar, & Kapler Smith, 2008; Herrera, Cellini, Barrera, Lencinas, & Pastur, 2018). Today, *P. nemoralis* is considered as being potentially invasive in some areas of North America, Australia and

New Zealand (CABI, 2020; Saul et al., 2017), threatening the local flora via either enhanced competition or elevating the fuel load of the woodland understorey (Dibble & Rees, 2005). However, there are no known intervention schemes to remove it.

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